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established in 1881

Spencer F. Baird
First U.S. Commissioner
of Fisheries and founder
of *Fishery Bulletin*

Discard mortality of black sea bass (*Centropristis striata*) in a deepwater recreational fishery off New Jersey: role of swim bladder venting in reducing mortality

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Abstract—The effects of barotrauma and other capture-related factors on the discard mortality of black sea bass (*Centropristis striata*) are poorly understood. The objective of this study was to estimate the discard mortality rate for black sea bass in the winter deepwater recreational fishery off New Jersey and to evaluate if swim bladder venting can reduce discard mortality. A total of 1823 fish were sampled at multiple depths (45, 58, and 67 m) from November 2016 through March 2017. To estimate discard mortality at a depth of 45 m, 96 individuals were tagged with acoustic transmitters and monitored with acoustic receivers. The majority (95%) of fish captured across all depths exhibited effects of barotrauma, which were more prevalent at greater depths. Results from longitudinal survival analyses indicate that venting was the most significant predictor of mortality at a depth of 45 m, with the estimated mean discard mortality rate being lower for vented (20%) than non-vented (49%) fish. Fight time had the largest statistical influence on the mortality of non-vented fish, whereas longer fight times (>54 s) resulted in higher mortality at a depth of 45 m. Discard mortality may have been higher at greater depths, but venting and other recommended practices can mitigate mortality at all depths sampled.

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Black sea bass (*Centropristis striata*) support valuable commercial and recreational fisheries in the United States along the East Coast and in the Gulf of Mexico (NMFS, 2018). In the northern stock area (i.e., Cape Hatteras, North Carolina, to Canada), the recreational fishery is frequently responsible for a significant proportion of the total catch (e.g., 61% of the total 2015 catch; NEFSC, 2017) over a wide range of environmental conditions, habitats, and depths. These diverse recreational fisheries for black sea bass are governed by a suite of regulatory measures (e.g., minimum size limits, daily retention limits, and seasonal closures) in both state and federal waters along the East Coast of the United States (ASMFC[1]).

The discard rate of black sea bass in U.S. recreational fisheries is frequently high, with 33–56% of all captured fish being discarded annually from 2010 through 2015 (NEFSC, 2017). Discard rates vary by state and region in response to regulatory measures, "high-grading" practices, or angler catch-and-release conservation ethics. The latest stock assessments and fishery management plans for black sea bass assume a 15% discard mortality rate for the coast-wide, year-round recreational fishery (NEFSC, 2017). However, published estimates of the discard mortality rate for this

[1] ASMFC (Atlantic States Marine Fisheries Commission). 2017. 2017 Review of the Atlantic States Marine Fisheries Commission fishery management plan for the 2016 black sea bass fishery; black sea bass (*Centropristis striata*), 12 p. ASMFC, Arlington, VA. [Available from website.]

species vary considerably by region and depth of capture (e.g., 4.7–39.0%), with an increase in discard mortality evident at greater capture depths (Bugley and Shepherd, 1991; Collins et al., 1999; Rudershausen et al., 2014).

As a physoclistous fish species, black sea bass often suffer from barotrauma when captured in deepwater (>35 m) recreational fisheries (Collins et al., 1999; Davis, 2002). Typical barotrauma effects experienced by physoclists are species-specific (Jarvis and Lowe, 2008; Hannah et al., 2014) but can include swim bladder expansion or rupture, exopthalmia, and stomach eversion (i.e., prolapse). Previous studies have demonstrated that even minor barotrauma can impair postrelease behavior, reduce submergence success, and result in high rates of discard mortality in many popular recreational species (e.g., Sauls, 2014; Curtis et al., 2015), including in black sea bass (Collins et al., 1999; Rudershausen et al., 2014). Fortunately, a growing body of evidence indicates that discard mortality can often be reduced by implementing barotrauma relief measures, such as swim bladder venting, or by using descending (i.e., release) devices to release fish at depth as opposed to at the sea surface (Drumhiller et al., 2014; Pulver, 2017; Runde and Buckel, 2018). Although the efficacy of venting and descending devices in mitigating mortality is fishery- and species-specific (Wilde, 2009; Curtis et al., 2015; Eberts et al., 2018), some evidence indicates that swim bladder venting is preferred and more likely to be practiced by recreational anglers because of its low cost and rapid application (Crandall et al., 2018).

Most of the recreational catch (75%) and discards (82%) in the northern stock of black sea bass were estimated to have occurred within state waters (i.e., <5.6 km, or 3 nautical miles, from shore) from spring through early fall during 2011–2015 (NEFSC, 2017). Popular recreational fisheries in the northeastern United States also target or catch black sea bass as bycatch in federal waters from the late fall through early spring. These fisheries predominantly occur at greater depths (>35 m), while black sea bass are carrying out their winter inshore–offshore seasonal migration (Moser and Shepherd, 2009). Although these deepwater fisheries account for a relatively small and uncertain proportion of total recreational catch of black sea bass (NEFSC, 2017), they provide valuable fishing opportunities for recreational fishermen during a season when relatively few species are available to target off the northeastern United States. Anecdotal reports suggest that many black sea bass captured in these deepwater fisheries experience moderate to severe barotrauma, but barotrauma relief measures (e.g., swim bladder venting) are neither required nor commonly practiced voluntarily. Furthermore, the extent to which environmental (e.g., cold water and air temperatures) and ecosystem (e.g., predator species and abundance) conditions influence black sea bass discard mortality during the winter in recreational fisheries off New Jersey is unknown.

Results of recent studies indicate that discard mortality rates in recreational fisheries are influenced by numerous biological, environmental, and technical factors (e.g., Capizzano et al., 2016, 2019; Weltersbach et al., 2019). Therefore, fishery- or region-specific estimates of discard mortality and recommendations for anglers for best practices in catch and release of black sea bass are required to provide the information needed for stock assessments, fishery management, and conservation efforts. The objective of this study was to estimate the discard mortality rate for black sea bass captured in the winter deepwater recreational fishery off New Jersey and to evaluate if swim bladder venting can reduce discard mortality.

Materials and methods

Study sites

Black sea bass were sampled at 3 deepwater sites off the coast of southern New Jersey from December 2016 through March 2017 (Fig. 1A). The primary study site was a shipwreck (site A) located ~85 km southeast of Sea Isle City, New Jersey, at a depth of 45 m and sampled from December 2016 through February 2017. At this location, consistently high rates of catch of black sea bass are produced at a depth range that is representative of common offshore fishing grounds for this species. To investigate how the condition of captured fish and discard mortality might vary by capture depth, sampling was conducted during February and March 2017 at 2 additional sites where the depths were 58 m (site B) and 67 m (site C), respectively.

Sampling

Prior to any sampling, an online survey of recreational black sea bass anglers and captains of vessels in this fishery was conducted during October and November 2016 to determine the reel type (e.g., conventional, spinning, or electric), tackle (e.g., line type and strength and hook type and size), and rigging techniques (e.g., leader material, length, and configuration) most commonly used in the winter recreational offshore fishery for black sea bass off New Jersey. This survey was primarily distributed through online message boards for recreational anglers. On the basis of results of this survey (number of respondents: 282), we chose standardized terminal tackle rigs for use on all tagging trips. These rigs consisted of a high-low rig (i.e., lead sinker at the bottom with 2 hooks attached above through dropper loops) made with 22.7-kg monofilament leader material and two 5/0-size octopus hooks (model 92553-BN, O. Mustad and Son[2], Gjøvik, Norway). The volunteer anglers were allowed to use their own rods and reels to represent the variety used by anglers under typical conditions. The retrieve (i.e., gear) ratios of all reels were recorded, ranged from 2.5:1.0 to 7.1:1.0, and were classified broadly as *low speed* (reel retrieve ratio <5.0:1.0) or *high speed* (reel retrieve ratio >5.0:1.0).

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

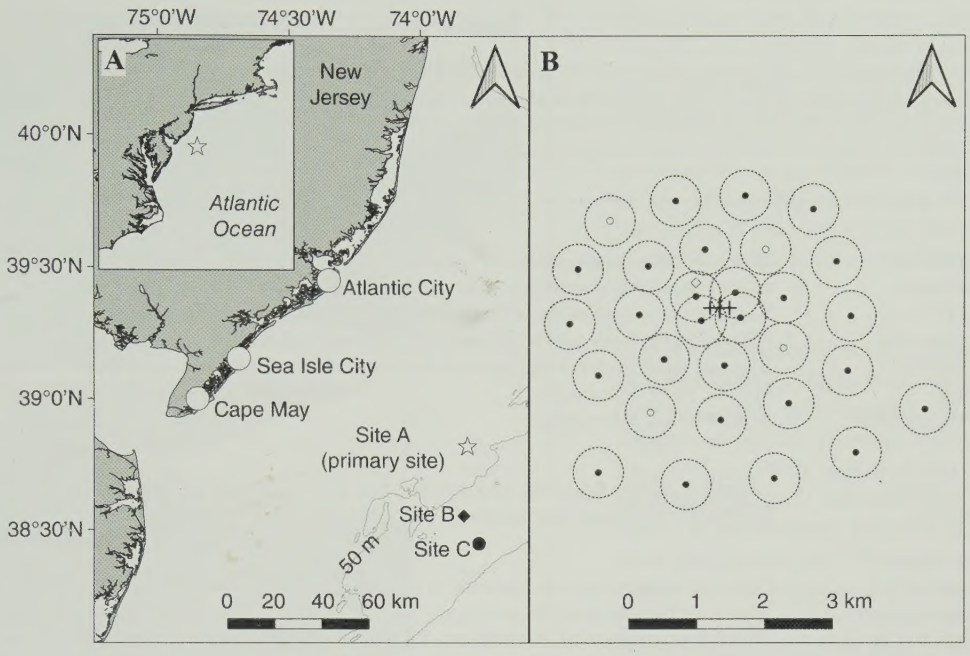

Figure 1

(**A**) Map showing the 3 locations (sites A, B, and C) where black sea bass (*Centropristis striata*) were sampled off the coast of southern New Jersey during December 2016–March 2017, with the primary site (site A) indicated with an open star in both the map and inset and the additional sites depicted by a black diamond (site B) and a black circle (site C). (**B**) The design of the acoustic receiver array that was deployed at the primary site to monitor the postrelease fate of the subsample of black sea bass that were captured around a shipwreck at a depth of 45 m and tagged with acoustic transmitters. Locations of individual acoustic receivers, with (open circles) and without (black circles) temperature loggers, deployed on mooring lines are presented. The dashed circles indicate estimated detection ranges for individual receivers. The stationary location of the acoustic transmitter attached to a mooring is indicated by an open diamond.

The sampling of black sea bass occurred during for-hire charters aboard the head boats F/V *Susan Hudson* (vessel length: 17 m) from Sea Isle City, New Jersey, and F/V *Porgy IV* (vessel length: 24 m) from Cape May, New Jersey. Each sampling trip had 6–14 volunteer anglers and up to 4 scientific personnel. Prior to starting fishing activity, each volunteer angler was required to complete a questionnaire that quantified their experience level with respect to saltwater fishing in deep water (depths >35 m). For all fishing activities, volunteer anglers were provided with the standardized terminal tackle rig, the same bait (Atlantic surfclam, *Spisula solidissima*), and a lead sinker (284–567 g) appropriately sized for the sea conditions, and they were allowed to determine how best to fish, handle, and unhook their catch to promote authentic scenarios. For each captured black sea bass, a series of technical and biological variables that describe the capture event were recorded (Table 1). Each volunteer angler was provided a stopwatch to record fight time, unhooking time, and handling time.

Anecdotal reports from anglers have suggested that the inability to submerge due to barotrauma is a major contributor to discard mortality. Previous research has indicated that swim bladder venting can reduce the rate of discard mortality for black sea bass captured at depths of 42–55 m off South Carolina (Collins et al., 1999). Therefore, to examine the efficacy of swim bladder venting for reducing discard mortality of black sea bass, a subset of fish was vented by using a Ventafish VF-1 Fish Venting Tool (Big Pond Products LLC, Tallahassee, FL) with a 16-gauge replaceable needle and 45° beveled front end. To standardize the methods, all fish were vented by a single trained scientist by placing the fish flat on a measuring board and inserting the needle into the swim bladder behind the pectoral fin following directions provided by the manufacturer. This approach was taken to examine the potential benefit of proper venting technique and to avoid potential bias that may occur from improper venting (Wilde, 2009).

Tagging procedure and postrelease fate monitoring

To monitor postrelease fate, a subsample of 96 black sea bass captured at site A (depth: 45 m) were externally tagged through the dorsal musculature with 69-kHz pressure-sensing VEMCO acoustic transmitters equipped

Table 1

Description of the technical, biological, environmental, and physical capture-related variables recorded for each captured black sea bass (*Centropristis striata*). The sampling of black sea bass occurred during for-hire charters operating from Sea Isle City and Cape May, New Jersey, between December 2016 and March 2017. Exopthalmia is an effect of barotrauma.

Variable (unit)	Description
Technical	
Capture depth (m)	Water depth at the location of capture
Angler experience	Angler experience score as classified by questionnaire (i.e., experienced or inexperienced)
Fight time (s)	Elapsed time from when a fish was hooked to when it reached the surface
Unhooking time (s)	Elapsed time from surfacing until the fish was unhooked
Handling time (s)	Elapsed time from surfacing until fish was released (time out of water)
Hook location	Mouth; body (foul hooked)
Hook removal method	Angler hand; mate hand
Biological	
Total length (mm)	Length from the tip of the snout to the tip of the center of the tail
Release behavior	Floating; swimming down; erratic swimming; sinking
Environmental	
Air temperature (°C)	On deck temperature at the time of capture
Surface temperature (°C)	Water temperature at the surface
Bottom temperature (°C)	Water temperature at the bottom or at the wreck
Delta temperature (°C)	Difference between surface and bottom water temperatures
Physical	
Injury	Present (1, >2 cm in length); absent (0)
Exopthalmia	Present (1); absent (0)
Stomach eversion	None (0); in mouth (1); protruding from mouth (2); ruptured (3)

with end caps (model V9P-2H, VEMCO, Bedford, Canada; dimensions: 29 mm long with 9-mm diameter; battery life: 673 d; pressure sensor maximum depth: 204 m; sensor resolution: 0.9 m; sensor accuracy: ±10 m). Transmitters were affixed to each fish by attaching a short piece of 22.7-kg monofilament to the transmitter's endcap and passing the monofilament through the dorsal musculature with a hypodermic needle. The transmitter was then secured in place by 2 Floy Petersen discs (Floy Tag Inc., Seattle, WA; 12.7-mm diameter) positioned on each side of the body (Fig. 2). Prior to at-sea sampling, a holding tank study was performed on captive black sea bass; this study confirmed that this attachment method resulted in no tag shedding or tagging-induced mortality over a 62-d period. Transmitters were programmed with a stepwise series of nominal transmission delay (120 s for 0–15 d; 300 s for 15–673 d). An equal number of vented and non-vented fish were tagged with acoustic transmitters (number of samples [n]=48, per treatment), and efforts were made to vent fish over all observed lengths and in an equal ratio across representative fishing conditions.

An array of 30 VEMCO VR2W 69-kHz acoustic receivers was strategically deployed around the shipwreck at site A to monitor the movements of black sea bass tagged with acoustic transmitters (Fig. 1B). To evaluate receiver detection range, a single V9P-2H transmitter was deployed on the bottom at a fixed location near the center of the array from January through March 2017. Analysis of detection data from this transmitter estimated the mean detection range (i.e., 50% probability of detection) to be 300 m (Winton et al., 2018). Twenty-five receivers were deployed for 119 d (28 November 2016–27 March 2017), and an additional 5 receivers were deployed for 69 d (17 January 2017–27 March 2017) along the southern extent of the array to better monitor fish emigration. HOBO Pendant temperature loggers (Onset Computer Co., Bourne, MA) were placed at the surface and bottom of the mooring lines of 4 receivers (Fig. 1B) and were programmed to record water temperature every 5 min (Table 1). Receivers were downloaded and cleaned every 30–45 d. Three receivers were lost during the study period.

To identify detection patterns indicative of a dead fish (i.e., continuous presence on the seafloor; see Yergey et al., 2012, and Capizzano et al., 2016), detection data were collected for 2 black sea bass that were intentionally sacrificed, tagged with acoustic transmitters, and released at the seafloor by using a descending device to minimize the risk of predation on the carcasses. These fish served as negative controls, and their detection histories were used to help identify mortality events in fish tagged with acoustic transmitters. In contrast, movement data obtained for 7 acoustically tagged black sea bass that were confirmed to be alive, either by acoustic detection in the Atlantic Cooperative Telemetry Network (n=4) or fishery-dependent recapture (n=3), were used as positive controls to distinguish behavior of black sea bass known to be alive.

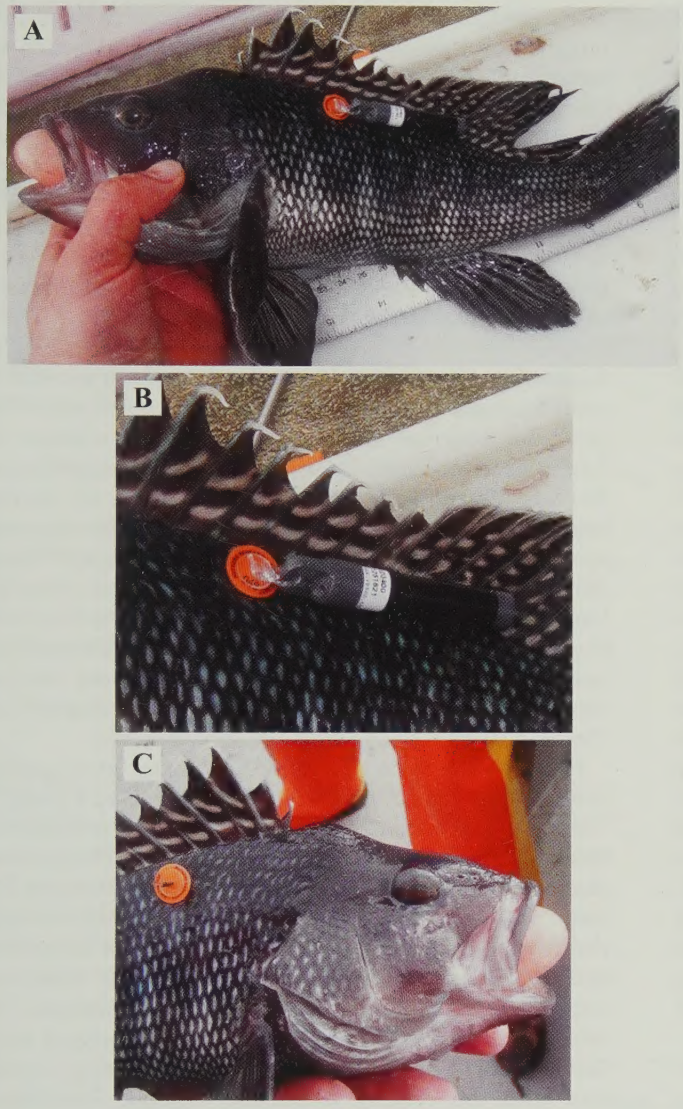

Figure 2

(**A**) Photograph of a black sea bass (*Centropristis striata*) externally tagged with an acoustic transmitter during this study. Fish were sampled for acoustic tagging off the coast of southern New Jersey from December 2016 through February 2017. A VEMCO V9P-2H acoustic transmitter with end caps is rigged with 22.7-kg monofilament and passed through the dorsal musculature of the tagged fish. Floy Petersen discs hold the tag in place on both sides of the fish: (**B**) one side is attached to the tag, and (**C**) the other side has a copper crimp that secures the tag in place.

Data analysis

A suite of models was employed to evaluate the effect of capture-related variables on discard mortality of black sea bass. Model selection procedures for identifying the most parsimonious model for each analysis in this study followed a stepwise forward selection procedure based on changes in the Akaike information criterion corrected for small sample sizes (ΔAICc) of 3 units or more (Burnham and Anderson, 2002) according to Benoît et al. (2010). Given the potential effect of individual angler behavior on results, an *angler* covariate was included as a random effect in all mixed-effect models to account for within-cluster correlation (e.g., Benoît et al., 2010; Knotek et al., 2018). All statistical analyses were performed in R (vers. 3.5.2; R Core Team, 2018), and statistical significance was accepted at a level of $P<0.05$.

Capture characteristics To investigate the relationship between fight time and several variables, including fish total length (TL), capture depth, capture as part of an event referred to as a *double header* (i.e., 2 fish captured simultaneously, 1 fish on each hook), and reel ratio (i.e., high or low speed reels), a generalized additive mixed-effect model with an inverse link function was performed by using the R package mgcv, vers. 1.8-26 (Wood, 2011). A mixed-effect logistic regression was also employed to evaluate the relationship between release behavior and several capture-related variables, including capture depth, TL, physical injury, presence of exopthalmia, presence of stomach eversion, and venting treatment.

Fate assessment The fate (i.e., alive or dead) of individual black sea bass tagged with acoustic transmitters was assessed by comparing vertical and horizontal movements against those of positive and negative controls. Prior to analysis, all transmitter data were initially vetted for false detections by using the false detection analyzer tool in VEMCO's User Environment (vers. 2.2.2) and irrational detection data that coincided with potential transmitter failures. Given the effect of misclassified mortality events in longitudinal survival analyses (described later), we employed a 3-step approach to determine the fate of individual fish. Step 1 involved the use of a discriminant function analysis, which creates a function capable of classifying individuals of unknown fate into groups based on metrics from individuals with known fates (White and Ruttenberg, 2007) by using solely acoustic detection data. A discriminant function was created by using gross movement metrics from positive and negative controls, specifically maximum depth variance, minimum depth, and the proportion of total depth observations that were shallower than an individual's mean overall observed depth minus the mean depth variance of the dead control fish. The discriminant function was executed by using the MASS package (vers. 7.3-45; Venables and Ripley, 2002) in R and resulted in a fate assignment for each fish.

Step 2 included the application of a variance test on depth observations recorded at defined intervals throughout the

detection history of each acoustically tagged fish (Capizzano et al., 2016, 2019). Only intervals with at least 10 observations were included in the analysis. To account for the effect of tide height on individual depth observations, the tidal cycle at site A was estimated and removed from each transmitter's depth record by using package oce (vers. 09-21; Kelley and Richards, 2017). The variance of tide-corrected depth observations in each time interval was individually compared with that of the negative controls for each fish by using a 1-tailed *t*-test of the absolute difference from the median (modified Browne–Forsythe test for homogeneity of population variance; Ott and Longnecker, 2010), hereafter referred to as the *depth-variance test*. Because of the occurrence of off-bottom movements in black sea bass, when the depth variance of a tagged fish was significantly different ($P<0.05$) from the negative controls during one or more time intervals, the fish was classified as being alive.

Following steps 1 and 2, all fish that were detected for >2 d and had the same fate predicted by both the discriminant analysis (i.e., step 1) and depth-variance test (i.e., step 2) ($n=50$) were assigned the appropriate fate. The final fate of the remaining detected fish ($n=44$), because of the brevity of their monitoring period (i.e., the lack of critical movement data for the depth-variance test) or the discrepancy between the discriminant analysis and depth-variance results, was determined in step 3 by using 1) a semiquantitative assessment of the horizontal and vertical movement patterns of each fish that placed particular emphasis on the comparison of their movements to those evident in both positive and negative controls and 2) an analysis of each fish's horizontal trajectory in relation to surface and bottom currents estimated at the study site by the Regional Ocean Modeling System (ROMS, vers. 3.6; Allen et al., 2003; ROMS/TOMS Group, 2013).

Briefly, if a fish's general pattern of movement was characterized by bottom-oriented behavior with some vertical movements and nonlinear horizontal emigration from the receiver array, it was considered to be alive. Fish were considered dead if they consistently remained at depth (i.e., on the seafloor) and made horizontal movements restricted to a straight line in the direction of the prevailing bottom current predicted by the ROMS model. In some instances, transmission data indicate more rapid horizontal movements and more frequent vertical movements of greater magnitude (i.e., 15–20 m off bottom) than were apparent in positive controls. These instances were considered predation events, a characterization that is consistent with reports from industry collaborators and with observations recorded during tagging that some fish are consumed by predators while being reeled up to the surface or while resubmerging postrelease. All fish with events identified as predations were included in the survival analysis as dead fish.

Longitudinal analysis Because the continuous acoustic monitoring of tagged black sea bass identified the time when fish either died or were last observed to be alive (i.e., longitudinal data), traditional survival analyses were used to address 2 objectives following procedures outlined by Knotek et al. (2018). The first objective was to evaluate the suitability of recorded capture-related variables (i.e., covariates) for predicting survival and then identify a parsimonious subset of those covariates that best predict survival. The second objective was to use this subset of covariates to assess whether potential models were capable of describing the survival function (i.e., cumulative probability of survivorship over time; Cox and Oakes, 1984) and estimating discard mortality of tagged black sea bass.

Evaluation of relevant capture-related factors for survival A combination of nonparametric and semiparametric longitudinal survival analyses were used to address the first objective. First, the empirical and nonparametric Kaplan–Meier (KM) estimator was used to visually explore the individual effect of capture-related covariates (Table 1) on the survival function (Cox and Oakes, 1984). For instances in which a categorical covariate had more than 2 groupings, and thus survival functions, the Peto–Peto modification of the Gehan–Wilcoxon log-rank test was used to evaluate if 2 or more survival functions were statistically different (Harrington and Fleming, 1982).

By reviewing the output of KM estimator plots and log-rank tests, 6 sensible covariates were selected a priori as variables that potentially influence discard mortality in black sea bass: fight time, handling time, TL, presence of physical injury, temperature differential between surface and bottom waters, and venting treatment. All other covariates that did not produce meaningful differences in their KM survival functions and log-rank tests were not considered and were dropped from the analysis. The release behavior covariate was dropped because of insufficient sample size among groups and its strong correlation with the venting treatment variable. Preliminary results from KM estimators and log-rank tests also support the categorization of various covariates, which was accomplished by either binning all continuous covariates of interest at their median value or combining groups in categorical covariates to produce meaningful associations (e.g., angler experience scores into experience categories). Such categorizations resulted in the addition of a 7th covariate, the general season of capture (i.e., astronomical autumn and winter).

Despite the KM estimator's ability to track the proportion of individuals considered to be alive at each time interval in the absence of censored observations, it provides a univariate analysis. Therefore, to objectively evaluate the additive effect of multiple covariates as predictors of survival, a mixed-effect Cox proportional hazards model (CPHM) was used to address the first objective (Cox, 1972; Therneau and Grambsch, 2000). A suite of CPHMs that incorporate all 7 covariates was constructed, and the CPHMs were compared by using a stepwise forward selection procedure with ΔAICc. Covariates that ultimately best fit the data were retained and used in the

second objective to both describe the survival function and estimate discard mortality.

Predicting discard mortality with relevant covariates Regardless of their ability to fit the data, nonparametric and semiparametric models cannot be used to parse out different mortality sources (e.g., capture and handling mortality and postrelease mortality) or provide mechanistic interpretations of survivorship patterns over time (Benoît et al., 2015). Therefore, the parametric modeling approach developed by Benoît et al. (2015) was used because of its ability to explicitly account for these types of mortality and to provide estimates for each. The survival function for this model, the probability of surviving to time $S(t)$, is expressed with the following equation:

$$S(t) = \tau \times \left\{ \pi \times e^{-[\alpha \times t]^{\gamma}} + (1 - \pi) \right\},$$

where τ = the probability of surviving capture and handling;
π = the probability that an individual was adversely affected by the fishing event postrelease; and
α and γ = the scale and shape parameters, respectively, of an underlying Weibull distribution that determines the mortality patterns over time for adversely affected individuals.

From this equation, we can understand that when t is 0, $S(t)$ is equal to τ. Therefore, as t increases to ∞, the expression $\tau \times \pi \times e^{-[\alpha \times t]^{\gamma}}$ decreases to 0 (i.e., all affected fish die) and $S(t)$ becomes $\tau(1-\pi)$ (i.e., only unaffected individuals remain alive). Additional details and justification of this model, including the use of maximum likelihood methods for fitting the data to the model, are provided in Benoît et al. (2012, 2015), and examples of this equation can be found in Capizzano et al. (2019).

After determining the basic model and appropriate terms to include, model variants of this equation were developed and fit with covariates of interest to address the second objective. The influence of covariates from the first objective that may affect survival are often introduced on τ and π terms in the model (e.g., Capizzano et al., 2016, 2019). Three model variants of this equation therefore were fit to the data (Table 2) and visually assessed by superimposing predicted survival functions on the KM estimates and 95% confidence intervals (CIs). Relative fit between model variants and selected covariates was quantified and compared with the stepwise forward selection procedure by using ΔAICc as previously described.

Evaluating relevant covariates for unvented subsample The nonparametric KM estimator and semiparametric CPHM survival analyses were also applied to data for unvented fish in the subsample of fish tagged with acoustic transmitters to examine the suitability of other covariates for predicting survival. Six sensible covariates previously included in the mixed-effect CPHM selection procedure were selected a priori and with evidence from KM estimators: fight time, handling time, TL, presence of physical injury, temperature differential between bottom and surface waters, and general season of capture (i.e., astronomical fall and winter). The angler covariate was included as a random effect. Despite the strengths of the parametric Weibull mixture distribution modeling approach described earlier, only the mixed-effect CPHM modeling procedure was used because sample sizes of fish were halved when examining only unvented fish.

Table 2

Three variants of the survival model developed by Benoît et al. (2015) to analyze the survivorship of black sea bass (*Centropristis striata*) over time and fit to data from sampling conducted off southern New Jersey between December 2016 and February 2017. Assumptions for parameters of the equation used to express the survival function (see the "Data analysis" section), specifically the probability of surviving capture and handling (τ) and the probability of being adversely affected by the fishing event postrelease (π), were used to define the 3 competing model variants. X=the design matrix for the covariates; β=the vector of parameters for the effect of the covariates.

Variant	Parameters	Description
1	$\tau = \left[1 + e^{\left(-X'\beta_1\right)}\right]^{-1}$ $\pi = \left[1 + e^{\left(-X'\beta_2\right)}\right]^{-1}$	Covariate effects on the probability of surviving capture and handling and the probability of being adversely affected by the fishing event postrelease
2	$\pi = \left[1 + e^{\left(-X'\beta_3\right)}\right]^{-1}$	Covariate effect on only the probability of being adversely affected by the fishing event postrelease
3	$\tau = \left[1 + e^{\left(-X'\beta_4\right)}\right]^{-1}$	Covariate effect on only the probability of surviving capture and handling

Results

Capture characteristics

Fifty volunteer anglers captured 1823 black sea bass (size range: 136–612 mm TL) (Table 3). Given the federal minimum landing size of 317.5 mm TL in 2017, 40% of the sampled fish would have been smaller than the legal limit. Forty-three anglers (86%) were classified as being *experienced* on the basis of their answers to our questionnaire and were responsible for the capture of 92% of the sampled fish. Capture-related variables were recorded for all fish with the exception of 110 fish that were retained for an aging experiment and had no venting status or release behavior recorded. A total of 957 fish had their swim bladder vented before release; 756 fish were released unvented. There were 321 capture events classified as a double header. The majority of fish (92%) were hooked in the mouth, but some fish were also foul-hooked in various locations of the body.

A total of 304 black sea bass (17%) incurred injuries (i.e., wounds >2 cm), mostly as a result of hooking trauma or the hook removal process. Twelve individuals (<1%) were dead upon landing, with most of them (n=8) having been bitten in half following predation by other fish. The vast majority of captured black sea bass (95%) exhibited effects of barotrauma, with a stomach eversion score of 2 (i.e., stomach protruding from the mouth cavity) present in 68% of all captured fish. Barotrauma effects were generally more prevalent in fish coming from greater depths, particularly exopthalmia, which was most prevalent at the deepest capture depth (Fig. 3).

Released black sea bass exhibited 4 behaviors, with the vast majority either swimming down (74%) or floating (25%). Only a small number of fish swam erratically (<1%) or sank (<1%). The prevalence of floating behavior was greater in fish captured at greater depths (Fig. 3).

Strong evidence from this study indicates that fight time increased in response to TL, capture depth, capture as part of a double header, and reel ratio (Table 4). Depth was the most influential factor affecting fight time, with fish captured at the deepest depth (67 m) experiencing the longest fight times. At each depth, interpolation of mean fight time indicates that fish >491 mm TL fought for longer than average durations. The results of a mixed-effect logistic regression indicate that TL, capture depth, venting, and the presence of exopthalmia weakly influenced release behavior, with fish having a lower probability of swimming down if they were larger in size, not vented, caught at greater depths, and experienced exopthalmia (Table 4, Fig. 4).

Table 3

Summary of capture variables from observations for all 1823 sampled black sea bass (*Centropristis striata*), including those for the 96 fish that were tagged with acoustic transmitters. Black sea bass were sampled off southern New Jersey between December 2017 and March 2017 at 3 sites with varying depths of capture (45, 58, and 67 m). Two methods of hook removal were used: angler hand and mate hand. Mean values are provided with standard deviations (SDs) in parentheses. The federal legal size limit for capture of black sea bass was 317.5 mm TL in 2017. An asterisk (*) indicates that water temperatures were available only for the primary site, a shipwreck located ~85 km southeast of Sea Isle City, New Jersey.

	Tagged fish		All observations	
Variable (unit)	Range	Mean (SD)	Range	Mean (SD)
Total length (mm)	278–546	354 (57)	136–612	339 (70)
No. fish at legal vs. non-legal size	–	–	1089/722	–
45 m	64/32	–	199/359	–
58 m	–	–	405/47	–
67 m	–	–	485/316	–
Fight time (s)	17–225	56 (24)	12–251	78 (32)
45 m	17–225	56 (24)	12–225	55 (22)
58 m	–		32–240	80 (27)
67 m	–		35–251	94 (30)
Unhooking time (s)	2–52	15 (11)	10–215	17 (19)
Angler hand	2–49	15 (11)	1–215	18 (20)
Mate hand	3–52	15 (12)	2–173	17 (17)
Experienced anglers	2–52	14 (11)	1–189	17 (19)
Inexperienced anglers	13–36	29 (9)	2–215	19 (21)
Handling time (s)	80–326	164 (51)	13–575	142 (81)
Air temperature (°C)	5.9–15.1	10.7 (2.3)	4.7–17.4	13.9 (2.4)
Sea surface temperature (°C)	7.4–13.8	11.4 (2.1)	7.2–13.9*	12.4 (1.7)*
Bottom temperature (°C)	7.4–13.8	11.3 (2.0)	7.5–13.4*	12.2 (1.4)*
Delta temperature (°C)	–0.6–0.4	0.1 (0.3)	–0.3–0.5*	0.3 (0.3)*

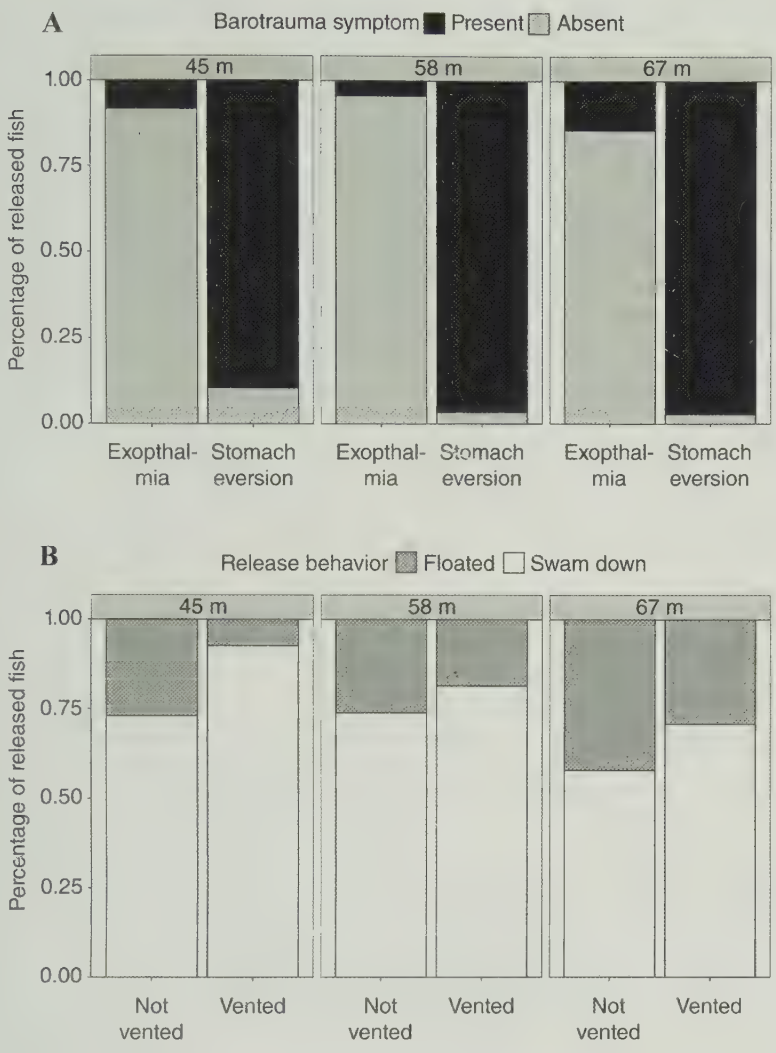

Figure 3

Stacked histograms depicting the prevalence of (**A**) barotrauma effects and (**B**) release behaviors of black sea bass (*Centropristis striata*) as a function of the depth (in meters) at which fish were sampled off southern New Jersey between December 2016 and March 2017. Stomach eversion was considered to be present if a fish was assigned a stomach eversion score of 1 (stomach everted but not protruding from mouth cavity), 2 (stomach everted and protruding from the mouth cavity), or 3 (stomach ruptured). Prevalence of behaviors is compared between fish that had their swim bladder vented and those that did not.

Survivorship assessment

Acoustic detection data were obtained for 94 of the 96 tagged black sea bass. The 2 fish that were not detected by the array were floating after release and were among the smallest individuals to be tagged with acoustic transmitters (286–287 mm TL). Of the 94 detected fish, 61 survived the capture, handling, and release processes and 33 died after release. Of those fish considered to be alive, 60 emigrated from the receiver array during the monitoring period, and the single fish that was detected within the acoustic array on the last day of monitoring (3 March 2017) was later detected by a receiver array off Maryland, confirming its survival. Of the 33 mortalities, 9 (27%) were attributed to predation following resubmergence (i.e., as the animal descended toward the seafloor or after it reached the seafloor). All predation events occurred between 1.8 and 18.4 h (mean: 7.2 h [standard deviation (SD) 4.5]) postrelease. The remaining 24 mortalities were assumed to have occurred as a result of the fishing event and occurred 5.0–128.0 h (mean: 17.1 h [SD 26.7]) postrelease (95.8% of mortality occurred within 72 h).

When examining the entire subsample of black sea bass for which acoustic data are available (n=94), the effect of venting treatment covariate was the only significant predictor of survival (CPHM approach; ΔAIC: 4.84) that primarily influenced the probability that a fish was adversely affected by the fishing event postrelease (Weibull mixture distribution modeling approach; Table 5, model variant 2). Most of the mortality of black sea bass was estimated to have occurred postrelease (Table 6), with mean rates of discard mortality for non-vented fish (49%; 95% CI: 32–63%) nearly 2.5 times greater than the rates for vented fish (20%; 95% CI: 11–35%) (Fig. 5).

With respect to the non-vented black sea bass (n=46) in the subsample, a mixed-effect CPHM found that the fight time variable best predicted survival for unvented fish (ΔAICc: 7.27). The CPHM's hazard ratio indicates that fight time was positively associated with the event probability (i.e., increased fight times increase the chance of mortality; P<0.05). For example, when the median fight time value (54 s) was used as a cut-off to form 2 groups, non-vented black sea bass that experienced fight times >54 s were estimated to suffer roughly 74% mortality, a much higher rate than the 29% mortality estimated for fish with fight times ≤54 s (Fig. 6).

Discussion

Our results indicate that swim bladder venting, when done correctly, reduced the discard mortality rate for black sea bass by almost 30% following capture at a depth of 45 m.

Table 4

Results of forward model selection for the generalized additive mixed-effect model used to examine the relationship between the capture-related variables and fight time and for the mixed-effect logistic regression model that evaluated release behavior against a set of sensible covariates for all released black sea bass (*Centropristis striata*) (n=1594). Covariates that produced a reduction of 3 or more units in the Akaike information criterion corrected for small sample sizes (AICc) from the previous model were retained. Values for the change in AICc from the previous candidate model (ΔAICc) are provided. Data used in the models are from sampling of black sea bass conducted off southern New Jersey between December 2016 and March 2017. An asterisk (*) indicates the model that best fits the data. Exopthalmia is an effect of barotrauma. TL=total length; DH=double header, an event when 2 fish are captured simultaneously, 1 fish on each hook.

Model	Estimated df	Deviance explained (%)	AICc	ΔAICc
Fight time				
~ 1	47.32	49.91	15688.16	595.88
~ s(TL)	48.29	54.24	15531.77	439.49
~ s(TL) + depth	49.46	63.10	15150.16	57.88
~ s(TL) + depth + DH	50.64	64.04	15105.86	13.58
~ s(TL) + depth + DH+ reel gear*	51.52	64.30	15092.28	0.00
Release behavior				
~ 1	47.32	1.98	1832.16	95.28
~ Depth	48.29	2.90	1783.03	49.13
~ Depth + venting	49.46	4.97	1747.24	35.79
~ Depth + venting + TL	50.64	5.47	1740.04	7.20
~ Depth + venting + TL + exopthalmia*	51.52	5.75	1736.88	3.16

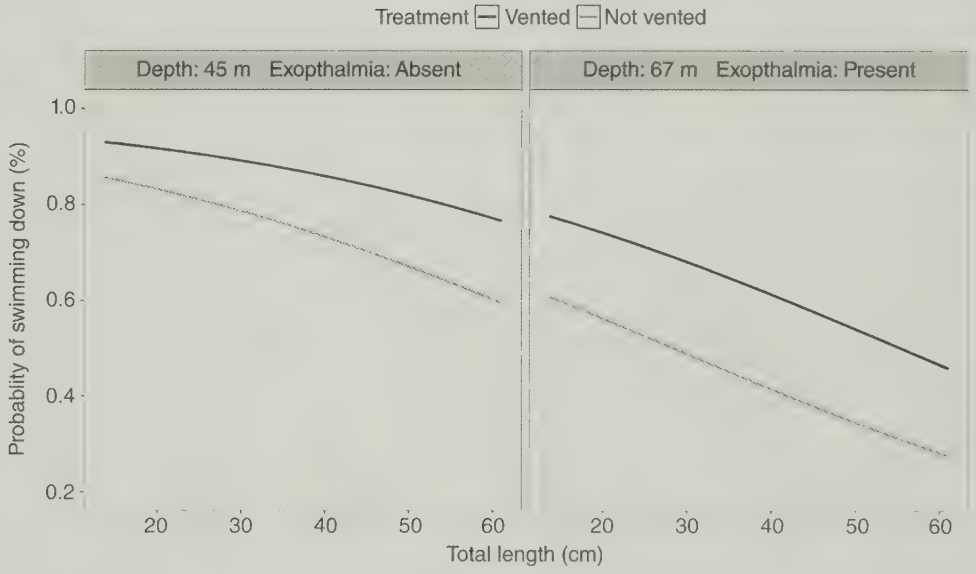

Figure 4

Probability that a released black sea bass (*Centropristis striata*) will actively swim down if it had its swim bladder vented (black line) or not vented (gray line), and how that probability varies by total length, depth of capture, and the presence of exopthalmia. Data used to model the probabilities came from fish sampled off southern New Jersey during December 2016–March 2017. For simplicity, 2 plots illustrate the overall submergence probability of fish with no exophthalmia captured at a shallow depth (45 m, left plot) in comparison to that of individuals with exopthalmia captured at a greater depth (67 m, right plot) by venting treatment and total length.

Table 5

Summary of results of model variant and covariate selection that used maximum likelihood and a forward selection procedure for the subsample of black sea bass (*Centropristis striata*) tagged with acoustic transmitters (n=96). Black sea bass were sampled off southern New Jersey at a depth of 45 m between December 2016 and February 2017. Values for the Akaike information criterion corrected for small sample sizes (AICc) and for the change in AICc from the previous candidate model (ΔAICc) are provided. An asterisk (*) denotes that the strongest evidence was for variant 2 of the model, which included the effect of venting covariate on the probability that a fish was adversely affected by the fishing event postrelease.

Run	Covariates	Variant	AICc	ΔAICc
1	~1	–	134.90	–
2*	~Venting	2	129.40	5.50
2	~Venting	1	132.52	2.38
2	~Venting	3	146.05	−11.15

These results are consistent with those from previous work that found that swim bladder venting reduced the discard mortality rate for black sea bass off South Carolina (Collins et al., 1999) and from a recent meta-analysis that found that swim bladder venting, as well as the use of descending devices, had positive effects and reduced discard mortality for fish of several species that experienced barotrauma (Eberts and Somers, 2017). Interestingly, the clear benefits of proper swim bladder venting presented herein are counter to previous assertions that this practice should be prohibited given the possibility that it may adversely affect the survival of fish captured from deep water (e.g., Wilde, 2009). Because of the detrimental effects of improper venting technique (e.g., Scyphers et al., 2013; Brownscombe et al., 2017), the benefit of swim bladder venting for reducing discard mortality of black sea bass in deepwater recreational fisheries will not be fully realized without the extensive education and training of recreational anglers on proper venting techniques. Accordingly, future research should evaluate the relative benefits of swim bladder venting against those of using descending devices for reducing discard mortality of black sea bass in order to develop recommendations for the most appropriate catch-and-release procedures, particularly given that 40% of the fish sampled were below the minimum landing size and would have been discarded under typical fishery scenarios.

Our collaborations with industry stakeholders in New Jersey indicate that offshore anglers or crewmembers on for-hire vessels that target black sea bass do not commonly practice swim bladder venting. Therefore, the estimate of 49% for the discard mortality rate of non-vented fish is most representative of the contemporary winter deepwater fishery when it operates at a depth of 45 m off New Jersey. This estimate of discard mortality is higher than previous estimates generated for non-vented fish captured over a similar depth range off South Carolina (39% mortality at depths of 43–54 m; Collins et al., 1999). However, this discrepancy could be in part a result of the fact that Collins et al. (1999) monitored the postrelease fate of fish for only 24 h while they were in cages, where animals were shielded from predation. In contrast, our electronic tagging approach enabled accounting for mortality occurring because of postrelease predation by fish of other species and documentation of delayed mortality up to 128 h after release. It is also possible that differing estimates of discard mortality rate were influenced by varying environmental conditions (e.g., air or water temperatures) between our winter study off New Jersey and the study completed by Collins et al. (1999) off South Carolina.

Table 6

Sample sizes and estimates of key parameters for the analysis of survival data for black sea bass (*Centropristis striata*) that had their swim bladder vented after capture at a depth of 45 m off southern New Jersey between December 2016 and February 2017. The numbers of fish that died upon release (dead), died during capture and handling or immediately after release (left censored), and were last observed to be alive (right censored) are presented. Estimates of the capture and handling mortality rate ($1-\tau$), the conditional postrelease mortality rate ($\tau\times\pi$), and the total mortality rate associated with the fishing event (i.e., discard mortality; $1-\tau+\tau\times\pi$) are presented by treatment group, with 95% confidence intervals provided in parentheses.

	No. of samples				Fishing mortality rates		
Treatment	Total	Dead	Left	Right	Capture and handling	Postrelease	Total
Vented	48	9	1	38	0.017 (0.001–0.158)	0.203 (0.107–0.351)	0.219 (0.131–0.406)
Not vented	46	18	5	23	0.017 (0.001–0.158)	0.487 (0.319–0.633)	0.504 (0.362–0.662)

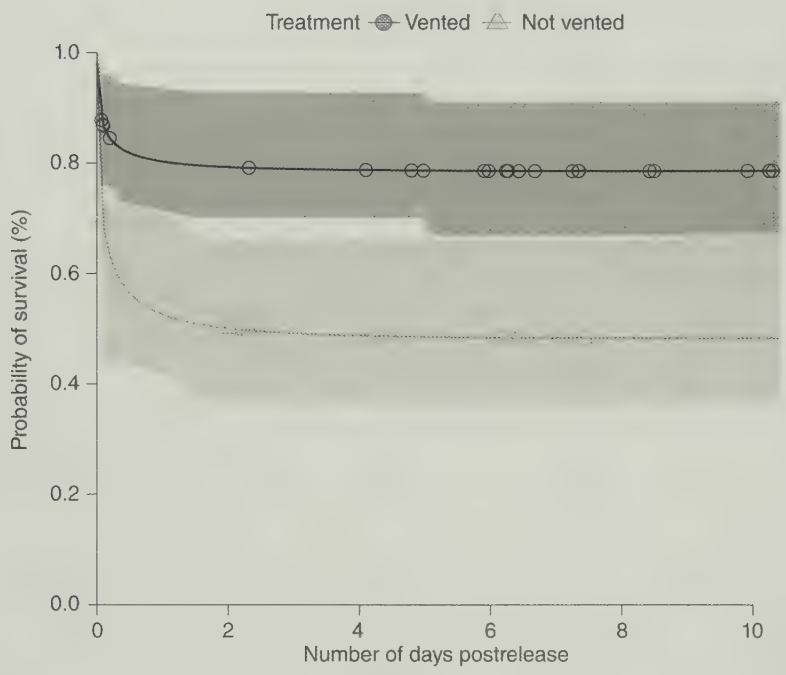

Figure 5

Nonparametric and model-based estimates of survival functions, cumulative probabilities of survival over time, for black sea bass (*Centropristis striata*) that had their swim bladders either vented (circles) or not vented (triangles) prior to release. Shaded areas indicate the 95% confidence interval for the estimates from the Kaplan–Meier survivor function, and the solid lines indicate estimates from the preferred survival model. The circles and triangles indicate the occurrence of observations in which the fish was last seen to be alive (right censored). The plot displays the fine-scale survival functions during the first 10 d after release, indicating that all of the discard-related mortalities were estimated to have occurred by day 5 given the asymptotic nature of the survival functions. Time zero is the time of release back into the water. Data used to produce estimates came from fish sampled off southern New Jersey from December 2016 through February 2017.

Postrelease predation had a noteworthy influence on the discard mortality rate for black sea bass, accounting for 27% of all documented mortality events. Results of previous research conducted off North Carolina indicates that predation of black sea bass during descent to the bottom may not greatly affect discard mortality (Rudershausen et al., 2014). However, on the basis of discussions with our industry collaborators and observations made during tagging, predation events can be common during the early part of the winter offshore fishing season off New Jersey (i.e., November and December) when predators, such as bluefish (*Pomatomus saltatrix*) and spiny dogfish (*Squalus acanthias*), are commonly present on the fishing grounds. Interestingly, no postrelease predation was observed for any acoustically tagged fish that was released after 21 December 2016, and no predation was observed during all trips to deeper fishing locations from mid-February through late-March of 2017. Therefore, predation on black sea bass by fish of other species both during capture and postrelease varied spatially and temporally, information that will be useful in consideration of fishery management options concerned with discards.

The practice of swim bladder venting was the single greatest predictor of discard mortality in the full subsample of fish tagged with acoustic transmitters, with unvented fish having lower submergence success than vented fish at all capture depths. Collectively, only 17% (2 out of 12) of the detected acoustically tagged fish that floated upon release ultimately survived, a rate that is consistent with the report by Rudershausen et al. (2014) that the inability to submerge did not result in 100% discard mortality. In addition, it is possible that the only 2 acoustically tagged fish not detected by any acoustic receiver experienced avian predation while floating at the sea surface. Avian predators, primarily herring (*Larus argentatus*) and great black-backed (*Larus marinus*) gulls, were abundant during the sampling trips during which these 2 fish were released, and these gulls were observed actively preying upon other released fish that did not have acoustic transmitters. Because the occurrence and prevalence of avian predation could not be fully accounted for during our study, actual discard mortality rates could be higher than those reported in this paper.

The latest stock assessments and fishery management plans for black sea bass assume a 15% discard mortality rate for the coast-wide, year-round black sea bass recreational fishery (NEFSC, 2017). Our results, as well as those of previous studies (e.g., Collins et al., 1999; Rudershausen et al., 2014), indicate that the discard mortality of black sea bass in deep waters is higher than the assumption that was applied in the last stock assessment. As a result, it is recommended that stock assessment scientists and fishery managers consider the higher discard mortality rates for deepwater fisheries in federal waters when quantifying total fishery removals and developing management measures. This is important for the winter offshore fishery because fishing effort and total catch during this season are not effectively monitored and estimates of discard mortality rates can factor heavily into different management options for recreational fisheries (e.g., the groundfish fishery in New England; Lee et al., 2017).

Our results add to the growing knowledge that capture depth has a large effect on discard mortality of black sea bass (e.g., Collins et al., 1999; Stephen and Harris, 2010; Rudershausen et al., 2014). For example, our estimate of the discard mortality rate for non-vented fish (49%) was

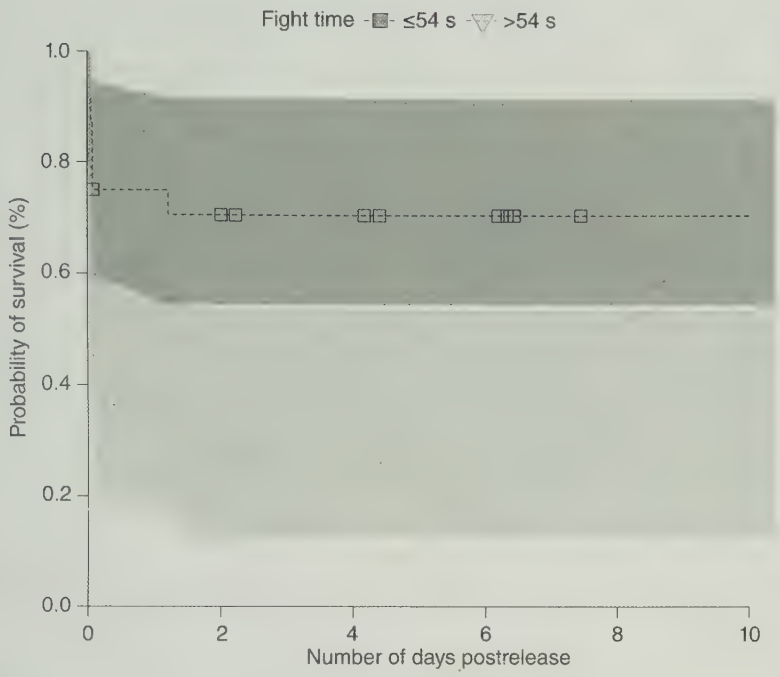

Figure 6

Plot of estimates (dashed lines) from the Kaplan–Meier survival function for black sea bass (*Centropristis striata*) in the subsample of fish tagged with acoustic transmitters that did not have their swim bladders vented (n=46), by low (≤54 s, squares) and high (>54 s, triangles) fight times. Shaded areas indicate the 95% confidence interval of estimates, and squares and triangles indicate the time when an individual was last observed to be alive (right censored). The plot displays the fine-scale survival functions for the first 10 d after release and eventual asymptote in survival. Time zero is the time of release back into the water. Data used to produce estimates came from fish caught off southern New Jersey between December 2016 and February 2017.

more than double the estimate (19%) of Rudershausen et al. (2014) for black sea bass captured at depths of 20–35 m, over 10 times greater than an estimate (4.7%) for black sea bass captured at depths of 6–12 m (Bugley and Shepherd, 1991), and comparable to estimates of immediate mortality (66%) following capture at depths >40 m (Stephen and Harris, 2010). On the basis of results of previous studies, it has been speculated that increased mortality at greater depths is attributable to barotrauma; however, results of our survival analysis on unvented fish captured at a depth of 45 m indicate that longer fight times also increase discard mortality. Therefore, it is likely that both vented and unvented black sea bass captured at depths greater than 45 m will experience higher discard mortality rates than reported herein because of both increased fight time and barotrauma. Additional research at depths greater than 45 m is needed to verify this assertion.

In contrast to previous studies, for example those by Rudershausen et al. (2014) on black sea bass and by Capizzano et al. (2016) on Atlantic cod (*Gadus morhua*), physical injury due to hook trauma or hook removal was not found to be a significant predictor of discard mortality for black sea bass. The vast majority of individuals (83%) did not experience hook trauma following a capture event, and there was a low incidence (<1%) of deep or internal hooking in the esophagus, viscera, or gills. This low incidence of deep hooking may result from the use of a high-low terminal tackle rig with short leaders from the main line to each hook (i.e., dropper loops of 7.6–12.7 cm). As suggested by Capizzano et al. (2016), this configuration does not leave much opportunity for the fish to swallow the hook and therefore results in a high incidence of mouth hooking. The use of circle hooks, which have been reported to increase the incidence of mouth hooking in other fisheries (see the review by Cooke and Suski, 2004), may not offer an appreciable conservation benefit for black sea bass, given the already low incidence of deep hooking observed with the high-low tackle rig and octopus hooks used in this study.

The survivorship assessment used to infer fate of individual fish was complex but warranted, given the variable acoustic detection histories evident for black sea bass of both known (i.e., positive and negative controls) and unknown fate. In previous studies, animal fate has been successfully reconciled by using solely the depth-variance test (e.g., for Atlantic cod; Capizzano et al., 2016) we employed in our study. However, when applied to our detection data, neither of these quantitative techniques was able to consistently predict the fate of all black sea bass (i.e., analyses with these techniques predicted different fates for nearly half of the detected fish), an outcome that was similar to that of previous work with haddock (*Melanogrammus aeglefinus*) in the Gulf of Maine (Capizzano et al., 2019). Because of this discrepancy, it was necessary to take a semiquantitative approach that both visually compared fish horizontal and vertical movements to those of positive and negative controls and predicted bottom currents in the study area to satisfactorily determine the fate of a large number of individuals. Although this approach lacked the full quantitative rigor of the depth-variance test, it was particularly effective at identifying predation events and at predicting the fate of fish with very short (i.e., hours) detection histories. Our methods can serve as a useful model for future studies, given that the analytical approaches for determining the fate of animals tagged with acoustic transmitters, as a part of discard mortality studies, frequently need to be developed specifically for a study and its unique factors, such as array design and animal behavior.

The successful identification of factors that influenced mortality, and therefore the discard mortality rate, of black sea bass in the winter offshore recreational fishery off New Jersey permitted formulation of recommendations for best practices in catch-and-release procedures aimed at reducing discard mortality. On the basis of the findings that swim bladder venting (when done correctly) was the most influential factor affecting discard mortality and that it increased submergence success over all depths (i.e., reduced the incidence of floating), we recommend that anglers vent all black sea bass before releasing them during the winter offshore fishery season. Given the finding that longer fight times (>54 s) increased mortality in the subsample of fish tagged with acoustic transmitters, another logical step is to explore methods to minimize the time black sea bass spend on the line while being reeled up to the surface.

Results of analysis with the generalized additive mixed-effect model indicate that capture depth had the largest influence on fight time; therefore, we recommend that anglers target black sea bass in water that is as shallow as possible. Although lower speed reels yielded longer fight times on average, the effect of individual angler had a seemingly large effect on the apparent relationship. In other words, angler behavior seemed to influence the effect that reel gear had on fight time more than the reel gear ratio itself. Given this finding, it is more logical (and practical) to recommend that anglers reel their catch to the surface at a moderate to fast pace, rather than to implement restrictions on reel gear. Capture as a part of a double header also resulted in increased fight time. Therefore, discard mortality may be reduced if anglers limit the number of hooks on their rigs. Also, we recommend that anglers use fishing gear (i.e., rod and reel or line) of appropriate strength for the area in which they fish to avoid unnecessary increases in fight time and discard mortality.

Acknowledgments

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Changes in the spawning distribution and biomass of Atlantic mackerel (*Scomber scombrus*) in the western Atlantic Ocean over 4 decades

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Abstract—The Atlantic mackerel (*Scomber scombrus*) has a wide distribution off North America that changes substantially seasonally and interannually, challenging attempts to track changes in stock size. We used egg collections to develop an index of spawning stock biomass for the southern contingent of Atlantic mackerel that spawns in U.S. waters. These results were combined with those from an egg survey of the northern contingent that spawns in the Gulf of St. Lawrence, Canada, to develop the only available stock-wide index. Egg production of Atlantic mackerel in the western North Atlantic Ocean has dropped >90% from the 1980s to the 2010s. The contribution of the southern contingent has generally been around 5–10%, except for during the late 1970s and early 1980s when it was 30–40%. On the continental shelf of the northeastern United States, there has been a northeastward shift in the distribution of eggs of Atlantic mackerel, with low levels of egg production recently at the historically important spawning location off southern New England. Overall, the index of spawning stock biomass generated from surveys in the waters of the United States and Canada provides a much needed means of tracking fluctuations in the biomass of this commercially valuable migratory species.

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The Atlantic mackerel (*Scomber scombrus*) is a migratory, small pelagic species that supports important fisheries throughout the North Atlantic Ocean. In recent decades, the majority of worldwide landings of Atlantic mackerel has occurred in the eastern Atlantic Ocean, where the challenges of assessing and managing this ecologically important species are well documented. Specifically, for Atlantic mackerel in the eastern Atlantic Ocean, a substantial increase in abundance and a shift and expansion in distribution started around 2005. This distribution change led to increased difficulty in surveying the population (Nøttestad et al., 2016), the development of new regional fisheries (Astthorsson et al., 2012), conflicts among nations in quota allocations (Spijkers and Boonstra, 2017), and potentially regional changes in the abundance of mackerel predators and prey (MacKenzie et al., 2014; Óskarsson et al., 2016). The results of a number of analyses indicate that the warming of waters in the North Atlantic Ocean is the cause of these changes (Hughes et al., 2014; Berge et al., 2015; Jansen et al., 2016). More recently, the assessment has indicated a decline in biomass of Atlantic mackerel in the eastern Atlantic Ocean and the need for quota reductions, presenting new assessment and management challenges.

Atlantic mackerel in the western North Atlantic Ocean have also shifted distribution, although the extent and causes of this shift are less certain than for Atlantic mackerel in the eastern Atlantic Ocean, as are the effects on resource surveys, stock assessments, and the availability of Atlantic mackerel to regional fisheries. Atlantic mackerel in the western Atlantic Ocean are considered a single population (Sette, 1950), with a southern contingent that spawns in U.S. waters offshore of southern New England and in the western Gulf of Maine (Berrien, 1978) and a northern contingent that spawns in waters of Canada, primarily in the southern

Gulf of St. Lawrence (Sette, 1943; Grégoire[1]). Results from tagging and cohort tracking work, primarily done in the 1930s (Sette, 1950), indicate that these 2 contingents mix on the continental shelf of the northeastern United States from the late fall through the spring but then separate during the late-spring spawning season and through much of the summer.

As with Atlantic mackerel in the eastern Atlantic Ocean, relative catches in different regional fisheries in the western Atlantic Ocean have changed over time, in part because of distribution shifts within the population. Additionally, across the entire western North Atlantic Ocean, there have been substantial multi-decadal cycles in landings, with a notable recent 88% decline between 2006 and 2015 to the lowest levels since the early 1800s (Hoy and Clark[2]; NEFSC, 2018). During this decline, only small portions of the quotas of both Canada and the United States were usually harvested despite industry capacity and market demand, leading to questions about why the industry was underperforming relative to expectations.

Two alternative hypotheses have been proposed to explain the decline in catch of Atlantic mackerel in the western Atlantic Ocean over the past 10–15 years. The first hypothesis is that warming waters in the western Atlantic Ocean (Shearman and Lentz, 2010) resulted in a shift in mackerel distribution that reduced availability to the fishery (Overholtz et al., 2011). This hypothesis of a change in distribution was supported by the results from a bottom-trawl survey conducted off the northeastern United States, results that included a northeastward shift in survey catch and mean abundance per tow near the highs of the time series (Overholtz et al., 2011). Similarly, a northeastward shift in landings of Atlantic mackerel in waters of Canada from Nova Scotia and the Gulf of St. Lawrence to Newfoundland (Grégoire et al.[3]) indicated that the distribution of Atlantic mackerel was changing. A stock assessment that estimated high biomass and very low exploitation rates of Atlantic mackerel in 2006 was consistent with the hypothesis that the population of Atlantic mackerel was robust but availability to the fishing industry had declined (NEFSC, 2006).

The alternate hypothesis is that a population decline, rather than a distribution shift, was responsible for the landings decline. This alternate hypothesis was supported by the decline in the index of egg abundance for Atlantic mackerel in the Gulf of St. Lawrence (northern contingent) (Grégoire et al.[4]), truncated age-structure in fishery catches despite low landings in both the United States and Canada, truncated age-structure in the U.S. bottom-trawl survey, and results of a stock assessment in 2016 in Canada indicating that the biomass of the northern contingent had reached a historic minimum in 2012 (DFO, 2017). A joint U.S.-Canada stock assessment conducted in 2010 was consistent with this view of the stock (Deroba et al., 2010), but that assessment was not incorporated into management decisions by either nation because of severe retrospective patterns in the assessment model and unresolved conflicts in the data, in particular between fishery catches and the index of abundance from the U.S. bottom-trawl survey.

One of the long-running challenges in assessing the stock of Atlantic mackerel in the western Atlantic Ocean is that the fishery-independent indices that are generally used for this stock, an egg survey in Canada (1982–present) and a bottom-trawl survey in the United States (1968–present), do not cover the entire range of this stock. Therefore, the trends in each index may be affected by changes in both abundance and availability associated with distribution shifts.

The egg survey in Canada uses the daily egg production method (Grégoire et al.[4]), a well-established approach that is used throughout the world (Bernal et al., 2012), including in the multi-nation triennial survey of Atlantic mackerel in the eastern Atlantic Ocean (Dransfeld et al., 2005). For the index of spawning biomass in Canada, a systematic plankton survey is used to develop daily egg production estimates, and gonadosomadic index measurements from landings are used to evaluate seasonality of spawning to scale daily egg production to annual egg production. Fecundity estimates are then used to calculate spawning stock biomass.

Within U.S. waters, there have been sporadic efforts, each with a slightly different analytical approach, to develop estimates of annual egg production or spawning stock size of Atlantic mackerel. These estimates include 64 trillion eggs and 320 million individuals in 1932 (Sette, 1943), 18 million individuals in 1966 (Berrien and Anderson[5]), 303 trillion eggs and 1220 million individuals in 1977 (Berrien et al., 1984), and 56 trillion eggs and 240 million individuals in 1987 (Berrien[6]). The 1987 survey was the only analysis to compare egg production in the United States and Canada in the same year, with only 10% of stock-wide egg production being

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estimated to occur in U.S. waters. After 1987, there was no further work on egg production of Atlantic mackerel in U.S. waters.

Our study focused on analyzing archived egg samples from a multipurpose plankton survey on the northeastern U.S. continental shelf, with the goal of creating a time series of egg production for the southern contingent of Atlantic mackerel. The specific objectives of this study were 1) to create a joint U.S.-Canada stock-wide index of spawning biomass for Atlantic mackerel that could be evaluated in stock assessments, 2) to estimate the proportion of spawning by each contingent, 3) to document shifts in the distribution of spawning by the southern contingent, and 4) to reanalyze historic egg data for Atlantic mackerel by using the same technique. The reanalysis of data from the 1930s and 1960s was undertaken to put the recent results into a broader historical context, because of questions about how the productivity of the stock has changed over longer time scales. This study was done in preparation for the stock assessment conducted by the Northeast Fisheries Science Center (NEFSC) in 2017 for Atlantic mackerel in the western North Atlantic Ocean (NEFSC, 2018); this stock assessment was supported in part by Fisheries and Oceans Canada.

Materials and methods

Field collections

Eggs from the southern contingent of Atlantic mackerel were sampled during the Marine Resources, Monitoring, Assessment, and Prediction (MARMAP) program, a long-term, fishery-independent monitoring survey, from 1977 to 1987 and during the NEFSC Ecosystem Monitoring (EcoMon) program from 1999 to the present (Richardson et al., 2010; Walsh et al., 2015). The MARMAP program sampled both fixed stations and random stratified stations, whereas the EcoMon program uses solely a random stratified design (Fig. 1). Both programs involved dedicated surveys, as well as operations integrated into interdisciplinary fall and spring bottom-trawl surveys.

At least 1 of the 6–8 shelf-wide yearly MARMAP cruises typically occurred during late April–June, the peak period of spawning of Atlantic mackerel, with 2 cruises occurring during the spawning season in 1987. As part of the EcoMon program, 1 of 6 seasonal surveys conducted in May or June coincides with spawning of Atlantic mackerel. The surveys completed before (bottom-trawl survey in March–April) and after (dedicated survey in August) the May or June survey rarely capture Atlantic mackerel in early life stages. Complete spatial coverage in the United States of the Atlantic mackerel spawning area, which includes the waters off the mid-Atlantic states, southern New England, and the western Gulf of Maine (Fig. 1), was achieved during surveys of the EcoMon program conducted in May or June in all years except 2003, 2008, 2012, and 2014.

All plankton tows of these surveys used a 61-cm bongo frame that was fished from the sea surface to within

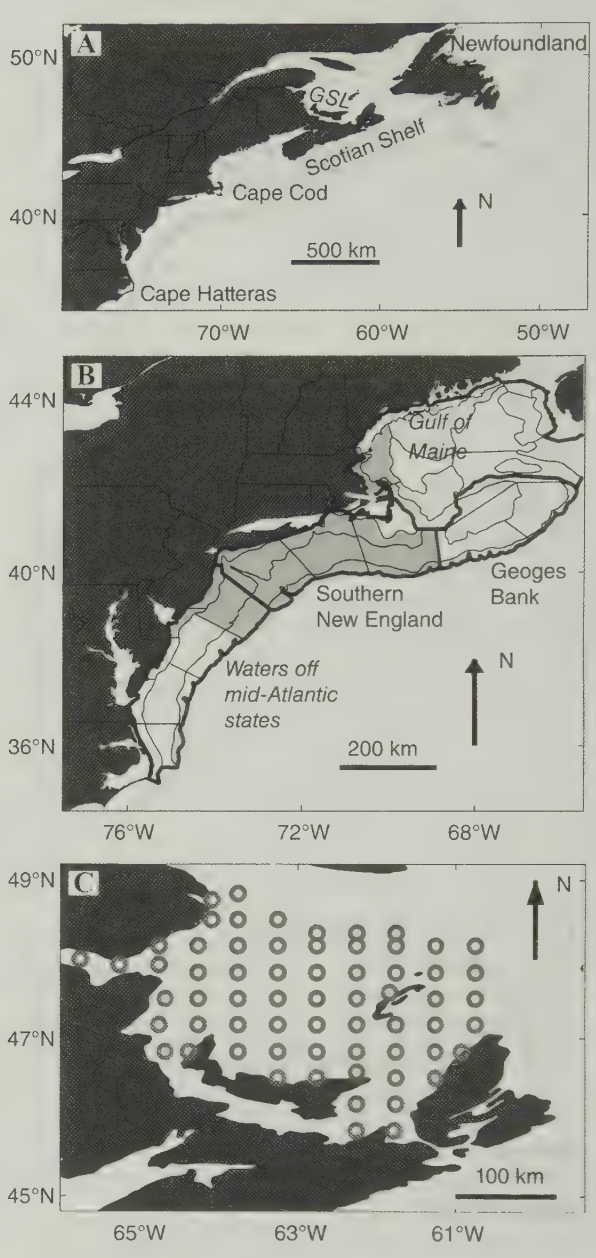

Figure 1

(**A**) Map of the western North Atlantic Ocean encompassing the range of Atlantic mackerel (*Scomber scombrus*) from Cape Hatteras, North Carolina, to Newfoundland, Canada. (**B**) Map of the sampling area for plankton surveys conducted by the Northeast Fisheries Science Center as part of the Marine Resources, Monitoring, Assessment, and Prediction program in 1977–1987 and the Ecosystem Monitoring program in 1999–2016. The 47 sampling strata are indicated with outlined boxes, along with the 4 labeled regions of the continental shelf (outlined in bold). The area shaded in gray indicates the core sampling area for the survey of eggs of Atlantic mackerel conducted as part of the plankton surveys. (**C**) Map of the station locations (open circles outlined in dark gray) of the egg survey conducted in the spawning area used by the northern contingent of Atlantic mackerel in the southern Gulf of St. Lawrence (GSL).

5 m of the seafloor or to a maximum depth of 200 m. Ichthyoplankton sampling used a 505-µm mesh net during MARMAP program surveys and a 333-µm mesh net during EcoMon program surveys. Eggs of Atlantic mackerel are >1 mm in diameter and are not extruded through either mesh size. All samples were fixed at sea in 3% formalin buffered with seawater.

The hydrography of the water column during the MARMAP and EcoMon program surveys was typically measured with an SBE 19[7], SBE 19plus, or SBE 19plus V2 SeaCAT conductivity, temperature, and depth (CTD) unit (Sea-Bird Scientific, Bellevue, WA) mounted directly above the bongo frame. A few exceptions to this method did occur. During MARMAP program cruises conducted in 1977 (NO7702 and DE7705), 1982 (AL8206), and 1987 (WI8701), low-vertical-resolution expendable bathythermographs (XBTs) were used. During cruise WI8701, water column temperatures were measured at every other station with an XBT and sea-surface temperatures were measured only at alternating stations. Additionally, at <1% of all stations, exclusive of 1987, temperatures for the full water column were not successfully measured, although sea-surface temperatures were recorded. All CTD data have been uploaded to the National Oceanographic Data Center (World Ocean Database, available from website) and can be accessed at the NEFSC ftp site.

Laboratory processing

Initial processing of most plankton samples, including the removal and enumeration of fish eggs, occurred at the Plankton Sorting and Identification Center in Szczecin, Poland. Eggs of Atlantic mackerel were then identified and developmentally staged at the NEFSC. All eggs collected during MARMAP program surveys were identified to the lowest possible taxonomic level (Berrien and Sibunka[8]). For the samples from EcoMon program surveys, only eggs of Atlantic mackerel were identified and staged.

Atlantic mackerel eggs can be distinguished from those of all other species at all stages of development, although there is some overlap in characters with eggs of cusk (*Brosme brosme*). The cusk is a rare species on the continental shelf of the northeastern United States, with eggs that have a textured rather than smooth outer chorion (Berrien, 1975). Egg staging for samples collected during EcoMon program surveys matched the criteria used in the egg survey in Canada: stage 1—fertilization to blastopore closure; stage 2—first appearance of the embryo to the embryo reaching half the circumference of the egg; stage 3—embryo extends from half to the full circumference of the egg; stage 4—embryo exceeds the full circumference of the egg to hatching; and stage 5—eggs unfertilized or dead eggs with an opaque look (Girard[9]). The criteria used to delineate stage-1 eggs were consistent across all sampling, but the definition of later egg stages differed between MARMAP program surveys and both the egg survey in Canada and the EcoMon program surveys. We restaged the later-stage eggs collected during MARMAP program surveys to match the criteria used in the survey in Canada. A subset of egg identifications and stages of the southern contingent of Atlantic mackerel were verified during an in-person collaboration with L. Girard at the Maurice Lamontagne Institute, Mont-Joli, Quebec; L. Girard performs all egg identifications for the egg survey conducted in Canada.

Calculation of egg production

Daily egg production (DEP) per unit area at each station was calculated by using the following equation:

$$DEP = Abundance\ (Stage\ 1\ and\ 5) \times \frac{24}{I}, \quad (1)$$

where *Abundance (Stage 1 and 5)* = number of eggs identified to be in stages 1 and 5 of development; and

I = the incubation time of stage 1 eggs in hours for a given temperature and is based on experimental work (Lockwood et al.[10]):

$$I = e^{(-1.61 \ln(T) + 7.76)}, \quad (2)$$

where T = the average temperature (in degrees Celsius) of the first 10 m of the water column.

For our analysis, this definition of T is consistent with data from the survey in Canada and with the vertical distribution of eggs of Atlantic mackerel in U.S. waters (Sette, 1943). Average temperatures at depths of 0–10 m were based on the concurrent CTD or XBT data, with sea-surface temperature used for the limited number of stations without measurements from the water column. We calculated the stratified mean daily egg production per square meter across the sampling area for each survey, and we scaled this mean to total daily egg production by using the total area of the sampled strata. Coefficients of variation for the stratified mean daily egg production were calculated by using the standard approach.

Spawning seasonality is used to estimate annual egg production from a measure of daily egg production. In the Gulf of St. Lawrence, seasonality of spawning is based on a logistic function fit to the average gonadosomadic index by day of year for individuals caught in the fishery (Grégoire et al.[4]). In contrast, the United

[7] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[8] Berrien, P. L., and J. D. Sibunka. 2006. A laboratory guide to the identification of marine fish eggs collected on the northeast coast of the United States, 1977–1994. Northeast Fish. Sci. Cent. Ref. Doc. 06-21, 162 p. [Available from website.]

[9] Girard, L. 2000. Identification of mackerel (*Scomber scombrus* L.) eggs sampled during abundance surveys in the southern Gulf of St. Lawrence. *In* The Atlantic mackerel (*Scomber scombrus* L.) of NAFO subareas 2 to 6 (F. Grégoire, ed.), p. 119–137. Can. Stock Assess. Secret. Res. Doc. 2000/021. [Available from website.]

[10] Lockwood, S. J., J. H. Nichols, and S. H. Coombs. 1977. The development rates of mackerel (*Scomber scombrus* L.) eggs over a range of temperatures. ICES CM 1977/J:13, 13 p. [Available from website.]

States fishery neither targets nor catches many Atlantic mackerel during the spawning season (<2% of landings in 2000–2015 occurred in May and June). Instead, we derived an average spawning seasonality function for the U.S. spawning ground from a larval index method (Richardson et al., 2010) that uses multi-decadal data on abundance at age of larval Atlantic mackerel to fit a larval mortality function, an annual index of larval abundance, and a 3-parameter skewed logistic function representing spawning seasonality:

$$P_D = \left(\frac{e^{a+bD}}{1+e^{a+bD}} \right)^{1/c}, \quad (3)$$

where a (−7.3110) = an estimated model parameter;
b (0.0694) = an estimated model parameter;
c (0.0828) = an estimated model parameter; and
P_D = the cumulative proportion of spawning at a day of year D.

The resulting spawning season represents the average for the time series rather than a year-specific estimate.

For the egg surveys in Canada and the United States, total annual egg production (AEP) is calculated by dividing the daily egg production (DEP) by the proportion of eggs estimated to be spawned on the mean day (D) stations were sampled on the survey:

$$AEP = DEP / (P_{(D+0.5)} - P_{(D-0.5)}). \quad (4)$$

Annual egg production on the continental shelf off the northeastern United States was also calculated for cruises undertaken in 1932 and 1966. These surveys provide an estimate of regional egg production prior to the substantial landings of the early 1970s. The sampling methods and laboratory work for these surveys differed from those undertaken during cruises of the MARMAP and EcoMon programs, and in some cases modifications to methods were required (Suppl. Material) (online only).

Calculation of spawning stock biomass

Spawning stock biomass (SSB) is calculated on the basis of total annual egg production (AEP) from the plankton surveys and annual fecundity from a reproductive study:

$$SSB = \frac{(AEP \times W)}{F \times R \times 10^6}, \quad (5)$$

where W = mean weight (in grams) of spawning fish;
F = mean female fecundity;
R = proportion female; and
10^6 = the value that converts grams to metric tons.

In the Gulf of St. Lawrence, annual fecundity is estimated on the basis of the measured weight of mature ovaries, which has been found to be a better predictor than length or body weight (Pelletier, 1986). Fecundity sampling of the southern contingent occurred in 1977 and 1987, with estimates of fecundity at length similar to values from surveys in Canada for Atlantic mackerel <35 cm in fork length (FL) but higher than those values for fish at larger sizes (Morse, 1980; Griswold and Silverman, 1992). In both U.S. studies, an allometric fecundity–weight relationship was also estimated. With an allometric fecundity–weight relationship, information on the size structure of spawners of just the southern contingent is required to calculate spawning stock biomass from a measure of total egg production; this information is unavailable. In calculating spawning stock biomass for the southern contingent, we used the annual fecundity estimates for the northern contingent of Atlantic mackerel.

Sensitivity analyses

The calculation of annual egg production for the southern contingent of Atlantic mackerel relies on parameters and functions that were derived from studies performed in other regions or different years. To the extent possible, we maintained consistency with the analysis used in the survey of the Gulf of St. Lawrence in order to create a single internally consistent stock-wide index. We used sensitivity analyses to evaluate the influence of different components of the calculations on both the trend and scale of the index.

Stage-specific egg incubation times are derived from laboratory experiments with a range of temperature treatments. Mendiola et al. (2006) repeated the study we used, Lockwood et al.[10], but sampled at more frequent time intervals and incubated eggs at lower densities, because of concerns about oxygen depletion. Both studies were done in the Bay of Biscay in the northeastern Atlantic Ocean. The equation for times of stage-1 egg development in Mendiola et al. (2006) was as follows:

$$I = e^{(-1.313 \ln (T) + 6.902)}. \quad (6)$$

These egg development times were shorter than those reported in Lockwood et al.[10] at all but the highest temperatures.

A common finding in studies of vertical distributions of eggs of Atlantic mackerel is that eggs occur mostly above the thermocline (Sette, 1943; Ware and Lambert, 1985; de Lafontaine and Gascon, 1989; Coombs et al., 2001). During sampling on the continental shelf of the northeastern United States, eggs were primarily within the upper 10 m of the water column (Sette, 1943), matching our use of the average water temperatures at depths from the surface to 10 m. We evaluated 2 alternative temperature measures in the incubation time calculations: sea-surface temperature and average temperature in the upper 20 m of the water column.

The calculation of daily egg production in the surveys in Canada and Europe does not adjust for mortality of eggs in stage 1 of development (Dransfeld et al., 2005; Grégoire et al.[4]). Egg mortality estimates based on field measurements range from 0.098/d to 0.540/d (Berrien et al., 1981; Kendall and Gordon, 1981; Thompson, 1989; Portilla et al., 2007). We used egg mortality estimates of 0.20/d and 0.55/d in our sensitivity analyses. Stage-1 egg abundances were scaled up by using a correction factor that corresponded to the number of eggs spawned (i.e., the

start of stage 1) versus the average number of stage-1 eggs at any point in time from spawning to the transition from stage 1 to stage 2:

$$Correction\ Factor = \frac{\left(\frac{I}{24}\right)}{\frac{1}{-Z}\left(e^{-Z\left(\frac{I}{24}\right)} - 1\right)}, \quad (7)$$

where Z = daily mortality rate; and
I = incubation time in hours.

This correction factor is applied on a sample-by-sample basis and varies on the basis of temperature-dependent incubation times.

Our spawning seasonality function was not estimated annually. We recalculated annual egg production with shifts in this annual spawning season of 14 and 7 d both forward and backward, for a total range of 28 d. For comparison, within the Gulf of St. Lawrence, the median day of spawning estimated through gonad sampling ranged from day 166 to day 179 (15–28 June) for a total range of 13 d (Grégoire et al.[4]).

We evaluated the effect of changes made in each of the 9 sensitivity analyses on the scale and trend of annual egg production. These evaluations included 1 analysis of egg development, 2 analyses of vertical distribution, 2 analyses of egg mortality, and 4 analyses of spawning seasonality. The annual egg production for each year in each sensitivity analysis was divided by the baseline for that year. The average of this metric quantifies the effect of each sensitivity analysis on the scale of annual egg production, and the standard deviation quantifies interannual variability in relative index values once the difference in scale is accounted for. We also plotted a time series of the relative difference in estimated annual egg production to evaluate the potential for a temporal bias in the index.

Distribution of spawning and spawning habitat

Egg distributions were mapped for 5 time periods spanning from 1977 through 2016. We also evaluated trends in the proportion of egg production that occurred in 4 regions on the continental shelf of the northeastern United States: the waters off the mid-Atlantic states, southern New England, Georges Bank, and the Gulf of Maine.

Quotient analysis was used to evaluate the preferred range of sea-surface temperatures for Atlantic mackerel spawning on the northeastern U.S. continental shelf (van der Lingen et al., 2001), an approach previously used to evaluate distributions of adult Atlantic mackerel during the U.S. spring bottom-trawl survey (Overholtz et al., 2011). The quotient for each 1°C temperature bin (Q_T) is calculated as follows:

$$Q_T = pM_T / pS_T, \quad (8)$$

where pM_T = the proportion of stations positive for eggs of Atlantic mackerel in each temperature bin; and
pS_T = the proportion of all stations in each bin.

Quotient values >1 indicate that a greater number of stations in the temperature bin were positive for mackerel eggs than was expected on the basis of sampling effort alone, with the significance of the quotient value obtained by using bootstrapping (Bernal et al., 2007; Overholtz et al., 2011).

We used the results of the quotient analysis and a NOAA 1/4° daily analysis, the Optimum Interpolation Sea-Surface Temperature (OISST) product (available from website), to quantify temporal trends in the area with sea-surface temperatures preferentially used by Atlantic mackerel for spawning. The OISST product interpolates measurements from a variety of different sampling methods to develop a map of daily, spatially resolved sea-surface temperatures (Banzon et al., 2016). We quantified the area with preferred spawning temperatures (Q_T>1) for each year from 1982 through 2016 in the waters off the mid-Atlantic states, southern New England, and the western Gulf of Maine on 19 May, the average peak day of spawning of Atlantic mackerel. Linear regression was used to evaluate trends in the preferred habitat.

Results

Egg distribution

The distribution of eggs of Atlantic mackerel on the continental shelf of the northeastern United States shifted northeastward between 1977 and 2015 (Fig. 2). In the late 1970s and early 1980s, the majority of egg production typically occurred in southern New England. By the early 2000s, the majority of egg collections occurred in the Gulf of Maine. Since 2010, there has been very little egg production in southern New England.

Significant quotient values >1 for eggs of Atlantic mackerel occurred at sea-surface temperatures between 7°C and 12°C. On average during 1982–2016, 65% of the core spawning area for Atlantic mackerel was in the temperature range of 7–12°C on 19 May. Over the period of 1982–2016, there was a decline in preferred spawning habitat of 0.5% per year, with the smallest areas occurring in 2012, 2013, and 2015. This decline was not significant (P=0.13), and interannual variability was high in the area with preferred sea-surface temperatures (Fig. 3).

Egg production and spawning stock biomass

Annual egg production on the northeastern U.S. continental shelf declined from a high of 213 trillion eggs in 1980 to a low of 653 billion eggs in 2011, with a minimal recovery occurring in recent years (Fig. 4; Suppl. Table 1 [online only]). The estimated spawning biomass of Atlantic mackerel on the continental shelf of the northeastern United States declined from a high of 390,000 metric tons (t) in the late 1970s to a low of 746 t in 2013 (Suppl. Table 1) (online only). In a reanalysis of historic data, annual egg production of the southern contingent, exclusive of the Gulf of

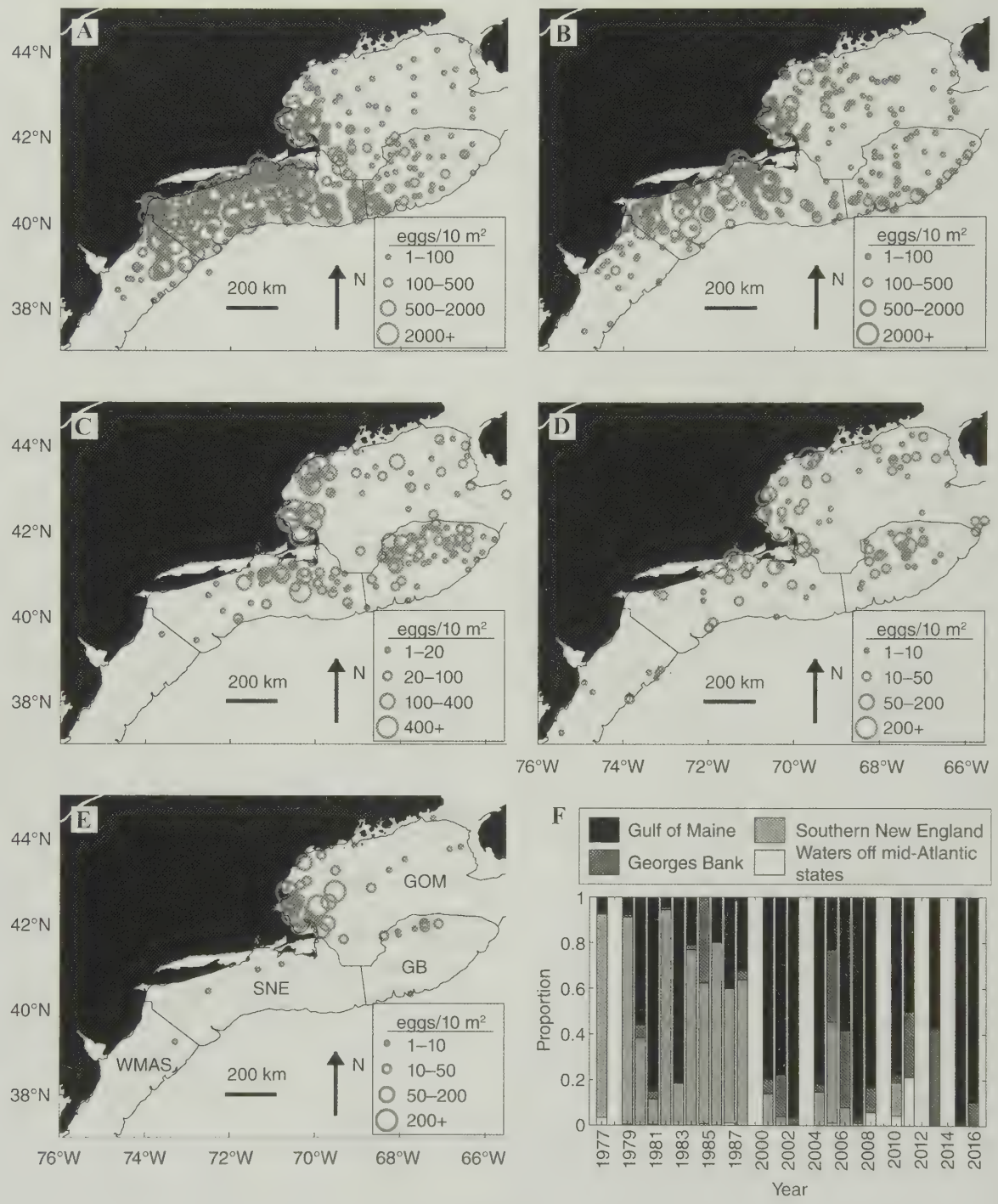

Figure 2

Distribution of eggs of Atlantic mackerel (*Scomber scombrus*) on the continental shelf of the northeastern United States over 5 time periods: (**A**) 1977–1982, (**B**) 1983–1987, (**C**) 2000–2004, (**D**) 2005–2010, and (**E**) 2011–2016. The size of open circles is scaled to the abundance of eggs. (**F**) The proportion of egg production by Atlantic mackerel in 4 regions is shown: waters off the mid-Atlantic states (WMAS), southern New England (SNE), Georges Bank (GB), and the Gulf of Maine (GOM).

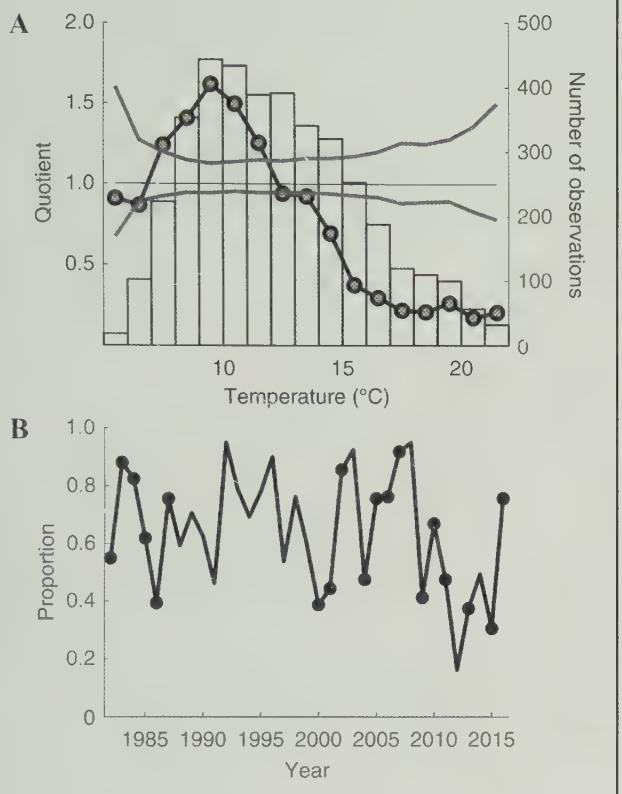

Figure 3

(**A**) Quotient analysis of sea-surface temperatures on the continental shelf of the northeastern United States where eggs of Atlantic mackerel (*Scomber scombrus*) were sampled in 1977–2016. Circles denote the quotient values. Gray lines indicate the 95% confidence intervals obtained by bootstrapping of the hypothesis that the quotient is equal to 1, and bars indicate the sampling effort within each temperature bin. (**B**) Proportion of the core spawning area used by Atlantic mackerel on the average peak day of spawning (19 May) that had temperatures within the range of temperatures preferred by Atlantic mackerel (7–12°C) as determined by the quotient analysis. Points indicate the years sampled during 1982–2016.

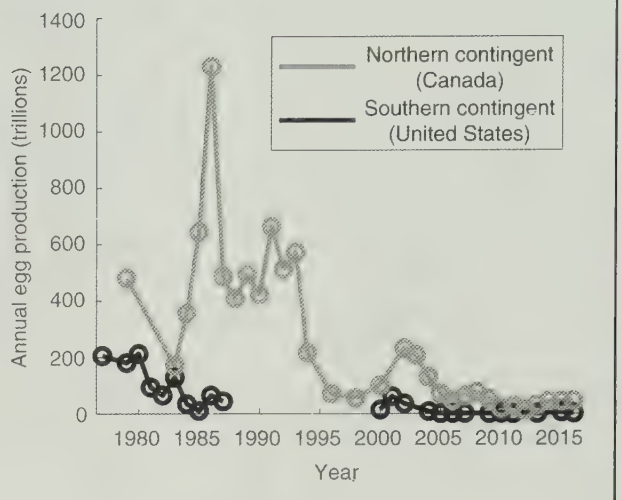

Figure 4

Annual egg production between 1977 and 2016 for 2 contingents of Atlantic mackerel (*Scomber scombrus*): the northern contingent that spawns in the southern Gulf of St. Lawrence, Canada, and the southern contingent that spawns on the continental shelf of the northeastern United States.

Maine, was estimated at 55.1 trillion eggs in 1932 and 12.7 trillion eggs in 1966, within the range of values seen during the past 4 decades (Suppl. Table 2) (online only).

Stock-wide estimates of annual egg production from the combined surveys in Canada and the United States declined approximately 55-fold from a high of 1290 trillion eggs in 1986 to a low of 22.4 trillion eggs in 2013. Despite some interannual differences in fecundity, estimated spawning stock biomass declined by a similar magnitude, from a high of 1.8 million t in 1986 to a low of 29,000 t in 2010. For most of the time series, the southern contingent accounted for 5–15% of the stock-wide egg production, with the exception of the first years of overlapping time series in 1979 and 1983, when the estimates were 27% and 43%, respectively (Fig. 4; Suppl. Table 1 [online only]).

Sensitivity analyses

Three sensitivity analyses focused on the time of egg development, with each of these changes having a minor effect on the scale and trend of estimates of annual egg production (Figs. 5 and 6). The substitution of an updated relationship of stage-1 egg development and temperature (Mendiola et al., 2006) increased the scale of egg production by 6% (standard deviation [SD] 5.4). Using sea-surface temperature rather than the average temperature of the upper 10 m of the water column reduced the estimated scale of egg production by 11% (SD 6.3), and using the temperature of the upper 20 m of the water column increased the estimated scale of egg production by 16% (SD 4.5). The results of these 3 analyses did not have obvious temporal patterns (Fig. 6).

Incorporating egg mortality (Z) into the calculations increased average annual egg production estimates by 24% (SD 5.0) with Z at 0.2/d and by 72% (SD 16.6) with Z at 0.55/d. The year-to-year variability in these estimates was relatively minor and can be attributed to differences in average incubation times among years leading to different cumulative mortalities of stage-1 eggs.

Changing spawning seasonality had a notable effect on the estimates of egg production. The use of a spawning seasonality function that shifted the peak day to 14 d earlier, from 5 May to 19 May, increased the average estimated annual egg production by 93% (SD 34.3), with notable year-to-year variability (Figs. 5 and 6). For all cruises since 2000, an increase in annual egg production was observed with this analysis because of the general timing of the survey near to or just after the average peak

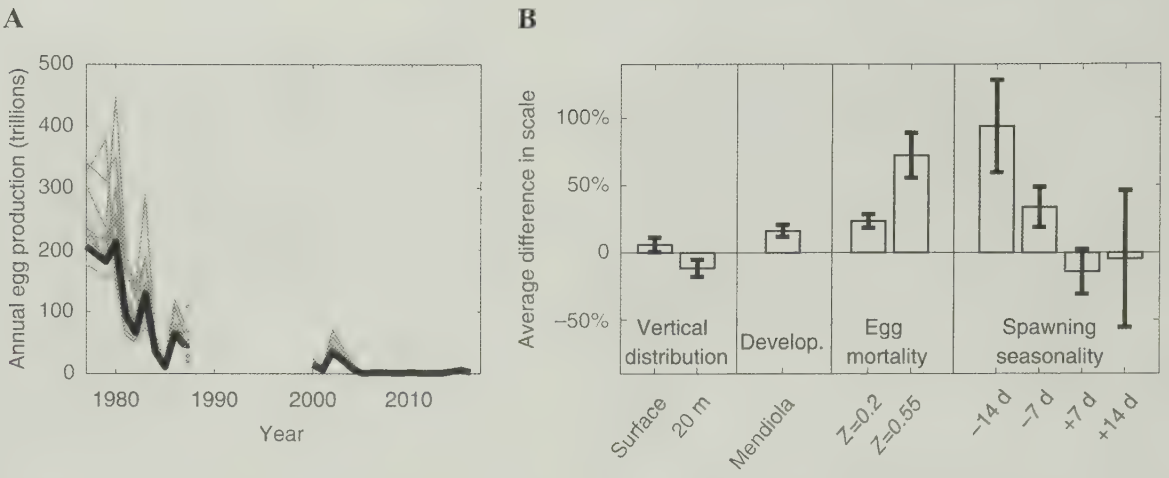

Figure 5

Results of sensitivity analyses conducted to evaluate the influence of 9 components on the trend and scale of a stock-wide egg production index for Atlantic mackerel (*Scomber scombrus*) on the continental shelf of the northeastern United States during 1977–1987 and 1999–2016. (**A**) Plot of the base index (black line) compared to indices resulting from all 9 sensitivity analyses (gray lines). (**B**) Average change in the scale of egg production for each of 4 sensitivity analyses that used one of these components: vertical distribution, egg development, egg mortality (Z), and spawning seasonality. Analysis of egg development used an equation from Mendiola et al. (2006) for calculations of the time of stage-1 egg development. Analysis of spawning seasonality shifted the season 7 or 14 d earlier or later. Error bars indicate standard deviations.

spawning period. A shift of the peak day to 7 d earlier increased the average scale by 35% (SD 14.9). Shifts of 7 d and 14 d later decreased the average scale by 14.0% (SD 16.7) and 4.7% (SD 50.8), respectively.

Discussion

Ichthyoplankton surveys have a long history of use in developing fishery-independent indices of abundance, particularly for migratory pelagic species that may otherwise be difficult to sample in a consistent manner across space and time (Lasker, 1985; Stratoudakis et al., 2006). The egg index we developed for Atlantic mackerel points to a severe decline in the southern contingent of the population in the western Atlantic Ocean over the past few decades, with a comparable decline when the egg indices based on collections in the United States and Canada are combined to evaluate the stock as a whole. The combined U.S.-Canada index potentially provides a more complete depiction of the stock of Atlantic mackerel in the western Atlantic Ocean because it is not as susceptible to changes in availability and seasonal migration patterns. The negative picture of stock trends is consistent with the substantial age-truncation in recent years despite historically low landings. Further evidence of a depleted population comes from observations by members of the commercial fishing industry and data that indicate that commercial landings are well below quotas and from a major decline in catch by the U.S. recreational fishery (which does not have size or bag limits) (NEFSC, 2018).

Potential error and bias in the egg index

A critical factor in evaluating any fishery-independent index is a thorough assessment of the magnitude of error in the index and the potential sources of bias in both the sampling and analytical techniques that produce the index. As with many other ichthyoplankton-based indices for schooling pelagic species, the egg index for the southern contingent of Atlantic mackerel was only moderately precise (average coefficient of variation: 0.4), as early-stage eggs tend to be patchy in their distribution. However, given the large magnitude of change in the index, concerns about potential sources of bias outweigh concerns about precision. The major change in field sampling protocol during the time series, a decrease in net mesh size from 505 µm to 333 µm, should not affect mackerel egg abundance measurements given their diameter (>1 mm) and the use of direct flow measurements. A change in personnel identifying eggs also occurred from early to late in the time series. This potential issue was addressed by training new personnel on previously identified eggs and through direct collaboration with Canadian scientists. Although not a direct comparison, low abundances of eggs of Atlantic mackerel in recent years were also evident in a study that genetically identified eggs preserved in ethanol (Lewis et al., 2016). Potential sources of bias in the analytical techniques were considered more

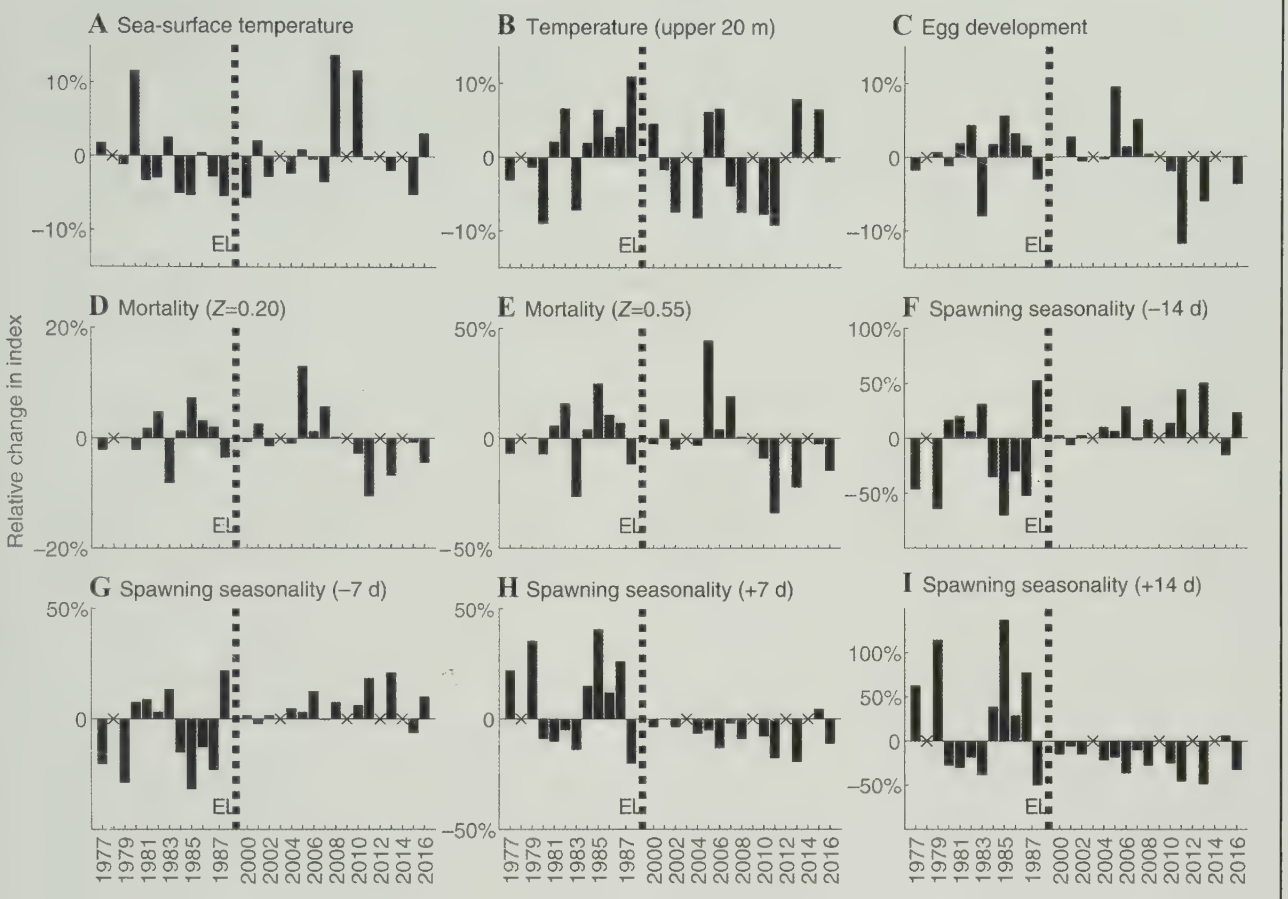

Figure 6

Relative change in the annual values of the egg production index (black bars) that results from sensitivity analyses conducted to evaluate the influence of 9 components on the index for the stock of Atlantic mackerel (*Scomber scombrus*) on the continental shelf of the northeastern United States during 1977–1987 and 1999–2016. Each analysis used one of the following 9 components: (**A**) sea-surface temperatures in the egg development equation, (**B**) temperatures averaged over the upper 20 m of the water column, (**C**) an alternate egg development equation, (**D**) integration of a daily egg mortality rate (Z) of 0.20, (**E**) integration of a Z of 0.55, and shifting of spawning seasonality to (**F**) 14 d earlier, (**G**) 7 d earlier, (**H**) 7 d later, and (**I**) 14 d later. Analysis of egg development used an equation from Mendiola et al. (2006) for calculations of the time of stage-1 egg development. The × symbols on the x-axis indicate years with incomplete sampling. The dashed vertical line indicates the break between the MARMAP and EcoMon programs. In 1987, 2 surveys were completed during the spawning season, an early survey (E) and a late (L) survey, with results reported separately.

likely to have occurred than field or laboratory biases and were evaluated by using sensitivity analyses.

The 3 sensitivity analyses that focused on egg incubation times revealed that uncertainty in the duration of stage-1 eggs had a relatively minor effect on both the scale and trend of egg production estimates. Both the equation we used for temperature-dependent stage-1 egg development time (Lockwood et al.[10]) and an alternative equation used in the sensitivity analysis (Mendiola et al., 2006) were based on studies of Atlantic mackerel in the eastern Atlantic Ocean, with only minor differences resulting from switching between the 2 equations. Total time to hatching (versus stage-1 duration) in a third study from U.S. waters (Worley, 1933) differed from that in the study by Lockwood et al.[10] by 5% on average across a temperature range of 10–21°C, indicating that the use of results from studies in the eastern Atlantic Ocean was appropriate. Sampling to resolve vertical distribution of eggs of Atlantic mackerel (e.g., Sette, 1943) occurred prior to the development of opening-and-closing plankton nets (e.g., Wiebe et al., 1976). Although the limited data on the vertical distribution of eggs of Atlantic mackerel leads to some uncertainty concerning the use of the average temperature at a depth from the surface to 10 m in the egg development equation, this uncertainty had only a minor effect on the index. In aggregate, these results indicate that lab studies to refine estimates of development times or field studies to resolve vertical distributions of eggs are of low priority.

The inclusion of egg mortality in the calculations led to an increase in estimates of the scale of egg production and spawning stock biomass. Effects on trends in the index were minor and driven by year-to-year differences in the temperature at which eggs were collected and, therefore, in the durations of stage-1 development. A number of early studies estimated egg mortality at low rates, and those results, combined with the short duration of stage-1 development of eggs, indicate that excluding this poorly estimated parameter results in only a minor underestimate in the calculation of annual egg production. In contrast, a recent study estimated mortality of stage-2 eggs at 0.54/d in waters of the eastern Atlantic Ocean (Portilla et al., 2007); it was not possible to directly estimate stage-1 mortality with that method. If this higher mortality estimate is accurate for mortality in the western Atlantic Ocean, the actual annual egg production, and in turn spawning stock biomass values, would be ≈70% higher than our estimates. Additional work to resolve egg mortality is, therefore, of primary importance if the scale of the estimated spawning stock biomass was to be directly used in a stock assessment or in development of management advice, rather than relative abundance indices, as is currently the case in both the United States and Canada.

Unlike the other changes evaluated in sensitivity analyses, results from varying the spawning seasonality function indicate that, if our assumptions are not correct, a temporal bias in the index could result. During 1977–1987, the seasonal timing of plankton surveys varied from year to year, and changes in spawning seasonality in the sensitivity analyses had both positive and negative effects on egg production estimates. Notably, in 1987, 2 cruises were completed, 1 cruise before and 1 cruise after the peak in spawning, and analyses of the data from both cruises yielded similar estimates of annual egg production. Since 2000, the window of late May–early June has been targeted for sampling; this sampling period is 1–2 weeks past the estimated average peak day of spawning. Shifting spawning earlier, therefore, resulted in a consistent increase in the index and vice versa, although the changes in index values did not change the conclusion that a severe decline had occurred in egg production of Atlantic mackerel.

The benefits of estimating spawning seasonality directly each year is clear from this sensitivity analysis. However, unlike for sampling in the Gulf of St. Lawrence, there is not a ready way to acquire a representative sample of adult Atlantic mackerel from the U.S. fishery during spawning. Periodically shifting the timing of the plankton sampling cruise earlier or sampling plankton during multiple cruises in a spawning season could address this issue, but such efforts would face logistical constraints. Importantly, sampling on the NEFSC spring bottom-trawl survey that operates from south to north from March through late April collects very few mackerel eggs and ripe adults. The signal of a substantial shift in spawning seasonality should be picked up on this cruise, but such a shift to date has not been observed. Additionally, direct measures of spawning seasonality in the Gulf of St. Lawrence have shown limited year-to-year variability with no evidence of a trend in the timing of spawning (Grégoire et al.[4]).

In developing the combined U.S.-Canada index for use in the stock assessment, we assumed that either only a small proportion of egg production occurs outside of the areas sampled or that this proportion does vary substantially over time. In U.S. waters, Atlantic mackerel do not occupy waters south of the southern boundary of sampling. Whether mackerel spawn in deep waters off the northeastern U.S. continental shelf is less certain, as this area has been sampled infrequently and only during certain seasons (Richardson et al., 2016). However, a 9–13 May 1993 cruise to this area did not collect larvae of Atlantic mackerel (Hare et al., 2001), and sea-surface temperatures off the shelf are generally >13°C during May. In contrast, sea-surface temperatures inshore of the sampling area are appropriate for spawning of Atlantic mackerel, and mackerel eggs have been collected in Long Island Sound, although at abundances lower than those of collections in offshore regions in the same year (Peterson and Ausubel, 1984).

The area inshore of the sampling domain is ≈7% of the total area of the shelf; therefore, much higher inshore egg abundances would be required to have a substantial effect on the index trends. Nonetheless, efforts to evaluate inshore spawning should be pursued. Within waters of Canada, exploratory cruises to the Scotian Shelf and the southern coast of Newfoundland in 2009 collected eggs of Atlantic mackerel but at levels that indicate the magnitude of spawning outside the Gulf of St. Lawrence was low (Grégoire et al.[11]). Sampling in waters of northeastern Newfoundland in 2015 and 2016 did not find mackerel eggs. Overall, there is no evidence of sufficient levels of spawning outside the sampling area to bias the combined U.S.-Canadian egg index, although exploratory cruises to potential areas used by Atlantic mackerel for spawning should be periodically pursued to further test this assumption.

The conversion of annual egg production to spawning stock biomass by using year-specific values of fecundity based on measured gonad weights presents one final source of uncertainty. Within the sampling in Canada, fecundity per unit of biomass was lower early in the time series, when the stock was high (average in 1980–1985: 520,000 eggs/kg), than later in the time series when the stock was low (average in 2010–2016: 890,000 eggs/kg), leading to a slightly more extreme decline in estimates of spawning stock biomass than the decline in annual egg production. In the United States, fecundity information was collected in 1977 and 1987, and these fecundity values relative to total length were very similar to those

[11] Grégoire, F., J.-L. Beaulieu, M.-H. Gendron, and D. LeBlanc. 2013. Results of the Atlantic mackerel (*Scomber scombrus* L.) egg survey conducted on the Scotian Shelf and Newfoundland's South Coast in 2009. Can. Sci. Advis. Secret. Res. Doc. 2012/127, 25 p. [Available from website.]

obtained in Canada for Atlantic mackerel with FL <35 cm but were higher in larger fish (Morse, 1980; Griswold and Silverman, 1992). As is the case with estimating spawning seasonality annually, estimating fecundity annually in the United States would be challenging but could reduce uncertainty and remove a potential source of bias.

Spatial distribution of egg production

Within the northeastern U.S. continental shelf, there has been a general northeastward shift in Atlantic mackerel egg distribution. This northeastward shift also has been evident in the sampling of adults on the bottom-trawl survey in March and April (Overholtz et al., 2011; Radlinski et al., 2013; Walsh et al., 2015), in the distribution of commercial landings during the winter and spring fishery (NEFSC, 2018), in the distribution of recreational catch, and not surprisingly, in the spatial patterns of larval Atlantic mackerel on the plankton survey (McManus et al., 2018). We sought to examine only whether the area of sea-surface temperatures preferred by Atlantic mackerel for spawning had declined because a fuller evaluation of larval mackerel habitat, which included concurrent zooplankton collections, has been performed by using data from the MARMAP and EcoMon programs (McManus et al., 2018). A slight decline in the area of suitable spawning temperatures was evident; however, this decline was not significant. The warming of waters on the shelf off the northeastern United States alone could not fully account for the near absence of eggs in some historical spawning areas, although these temperature changes likely have contributed to some of the observed distribution shift. Results from the more complex larval distribution models similarly indicate that, although there has been some decline in habitat of Atlantic mackerel, this decline could not account for the drop in larval abundance or the restriction of the spawning area in recent years.

At a broader spatial scale, our results indicate that the majority of spawning of Atlantic mackerel occurred in the Gulf of St. Lawrence in all years analyzed since 1979 and that the relative importance of the spawning ground in the Gulf of St. Lawrence has increased over the past 4 decades. This finding of a dominant spawning ground in Canada since 1979 contrasts with the conclusions of Sette (1943) that 90% of spawning in the early 1900s occurred in U.S. waters, based on a comparison of egg numbers in the United States during 1927–1932 to those from a survey conducted in the Gulf of St. Lawrence in 1914–1915. In addition to the differences in the years of sampling, there were issues with the sampling done in Canada in 1914–1915 that made the results of these comparisons highly uncertain, including unrecorded tow times leading to unknown water volume sampled for some stations, haphazardly spaced stations, the reliance on only tows of neuston nets (Sette, 1943), and the absence of tows in many areas of the Gulf of St. Lawrence that have supported higher egg abundances in recent decades (Grégoire et al.[3]).

Our reanalysis of the data from the cruise undertaken in 1932 in the United States, which used a different method, produced a similar estimate of annual egg production on the northeastern U.S. shelf (≈55 trillion eggs; 100,000 t of spawning stock biomass) as the original Sette (1943) analysis. Interestingly, the level of U.S. egg production in 1932 was similar to estimates for 1985–1987 in U.S. waters (mean: 51 trillion eggs), and population-wide landings were also comparable (78,000 t in 1932; mean of 73,000 t for 1985–1987) (Hoy and Clark[2]; NEFSC, 2018). However, the results of surveys in 1987 indicate that >90% of spawning occurred in the Gulf of St. Lawrence rather than the 10% that was suggested to have occurred in 1932. Comparison of survey data from these 2 time periods indicates that either fishing mortality of the entire stock was much higher in the early 1930s than in the late 1980s (i.e., similar landings but a lower total stock biomass) or that a much higher percentage of spawning occurred in Canada in the early 1930s than was originally estimated.

Given the lack of clear age truncation in the 1930s (Sette, 1950) and the caveats about the sampling in the Gulf of St. Lawrence during 1914–1915, caution should be applied in concluding that the dominant spawning site for Atlantic mackerel has switched from U.S. waters to Canada waters over the past century. On the other hand, comparative U.S.-Canada data from 1979 and 1983 do indicate that spawning in the United States was closer in scale to spawning in Canada during that time period, with the high levels of spawning occurring in the United States as early as 1977 but not in 1966. Overall, these results indicate that there has been a shift in recent decades to the northern contingent accounting for a higher proportion of spawning by the entire stock, but our findings leave unanswered the question of whether there are periods when the southern contingent is dominant.

Both environmental factors and population characteristics, such as abundance and length structure, have been observed to underlie changes in fish distribution and spawning distribution through time (MacCall, 1990; Bell et al., 2014; Secor, 2015). Both the northern and southern contingents of Atlantic mackerel in the western Atlantic Ocean have experienced a shrinkage in spawning area as the stock has declined and age structure has become truncated, changes that are consistent with MacCall's (1990) basin model of habitat selection. In the eastern Atlantic Ocean, there has been an expansion in the extent of the spawning area used by Atlantic mackerel as the stock has increased in abundance; however, even when temperature and abundance have been accounted for, it has not been possible to explain all the changes in spawning distribution (Brunel et al., 2018). Patterns on both sides of the Atlantic Ocean indicate that a complexity of factors underlie the observed changes in distribution (McManus et al., 2018).

In the western Atlantic Ocean, one factor that we have little understanding of but that likely affects broad-scale spawning distribution is how the spawning grounds in the Gulf of St. Lawrence and the United States are connected. Sette (1950) stated that interannual stability

in the migration patterns of specific year classes indicates a strong degree of fidelity by individuals to spawning grounds but that there was a lack of evidence for or against intergenerational stability in migration. The question of whether the northern and southern contingents are different populations persists to this day because there is no evidence of genetic differentiation or natal homing. Egg abundance in waters of Canada increased for many years after the 2 dominant year classes over the past 35 years (i.e., the year classes of 1982 and 1999) reached maturity; a similar increase in egg production has not been observed for Atlantic mackerel in U.S. waters. Results from reproductive sampling also indicate that these 2 year classes made up a majority of spawners in waters of Canada and that the 1982 year class was not a dominant influence in U.S. waters (Griswold and Silverman, 1992). Some stability year-to-year is likely to be observed in the relative magnitude of spawning in the 2 spawning grounds, stability driven by the fidelity of strong year classes to different spawning grounds. Whether the current pattern of dominance by the spawning ground in Canada will persist is tied in part to the sporadic recruitment of year classes to the 2 contingents, a process that is poorly understood and likely will remain difficult to predict.

The ultimate purpose of this work was to contribute to a stock-wide index of abundance for Atlantic mackerel in the western North Atlantic Ocean that could be incorporated as a fishery-independent index into the U.S. stock assessment completed in 2017. Because of disparate data sources in the previous assessment done in 2010, the model was not accepted for providing management advice, and subsequently the status of Atlantic mackerel in the United States was officially designated as *unknown*. The assessment model used in 2017 included additional years of catch-at-age data indicating continued age truncation (e.g., very few age-7 and older fish have been encountered since 2012) despite low landings. The joint U.S.-Canada egg-based estimate of spawning stock biomass was also included as a relative index (NEFSC, 2018). The results from the model used in 2017, which indicate very low population levels, was consistent with a broad consensus on the status of the stock and was ultimately accepted for management advice. Going forward, it is important to continue the field sampling and laboratory work that are essential to maintaining the egg index, while developing new studies that can address some of the uncertainties in this approach.

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Ichthyoplankton of the central North Atlantic Ocean: larval development of lanternfish species (Pisces: Myctophidae)

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Abstract—We present data on the morphology of the larval stages of lanternfish species (Myctophidae) in the central North Atlantic Ocean. This work is based on materials collected during 2 cruises in the North Atlantic Ocean from the equator to latitude 30°N in 2016 and 2018. Several larvae obtained in other geographical areas were used for identification. In total, at least 33 species of the Myctophidae were found in the study area. We provide descriptions of those species whose early development was not previously known and of those species whose morphology differs from those already described in literature: roundnose lanternfish (*Centrobranchus nigroocellatus*), stubby lanternfish (*Bolinichthys supralateralis*), *Diaphus* sp. 1, *Nannobrachium* sp. 1, noble lanternfish (*Lampanyctus vadulus*), and *Lampanyctus* sp. 1. The characteristics on which these determinations are based are discussed.

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Lanternfish (family Myctophidae) are the main part of the trophic chain of oceanic fish species and play a significant role in the feeding of commercially important species (Nafpaktitis et al., 1977; Sabourenkov, 1992; Kozlov, 1995). Because some species of lanternfish form large schools at certain periods of their life, this family can be considered to include prospective species for fisheries in the future (Ahlstrom et al., 1976; Valinassab et al., 2007). At least 80 species of myctophids inhabit the waters of the central North Atlantic Ocean, and early life stages are known for only 60% of these species. At least 33 taxa of Myctophidae belonging to 15 genera were caught in 2 complex faunistic expeditions conducted by the Institute of Oceanology, Russian Academy of Sciences (IO RAS), to the North Atlantic Ocean: the 39th voyage of the RV *Professor Logachev* and the 43rd voyage of the RV *Akademik Vavilov*. Larval identification is complicated by small specimens and the absence of transforming stages. Still, 28 of the 33 taxa were identified to the species level.

In earlier work, we considered the species composition and distribution of ichthyoplankton, including the larvae of lanternfish collected during 43 voyages (Bolshakova and Evseenko, 2020). This article presents larval descriptions for species and genus-level types previously undescribed for the region, including the stubby lanternfish (*Bolinichthys supralateralis*) and the roundnose lanternfish (*Centrobranchus nigroocellatus*), and for taxa, such as *Diaphus* sp. 1, *Nannobrachium* sp. 1, and *Lampanyctus* spp., for which determination poses difficulties.

Materials and methods

Early developmental stages of fish sampled during the 43rd expedition of the RV *Akademik Vavilov* and the 39th expedition of the RV *Professor Logachev* served as materials for the work we present here. A representative faunistic collection of ichthyoplankton and adult fish was taken in the cross-section between latitude 30°N and the equator in October 2016 and in a polygon in the central part of the North Atlantic Ocean in March 2018 (Fig. 1). Additionally, materials from the collections of the 29th expedition of the RV *Akademik Ioffe* to the central and South Atlantic Ocean and the 36th expedition of the RV *Akademik Kurchatov* to the West Indian Ocean were used (Table 1). The ichthyoplankton was sampled by using an Isaacs-Kidd mid-water trawl with

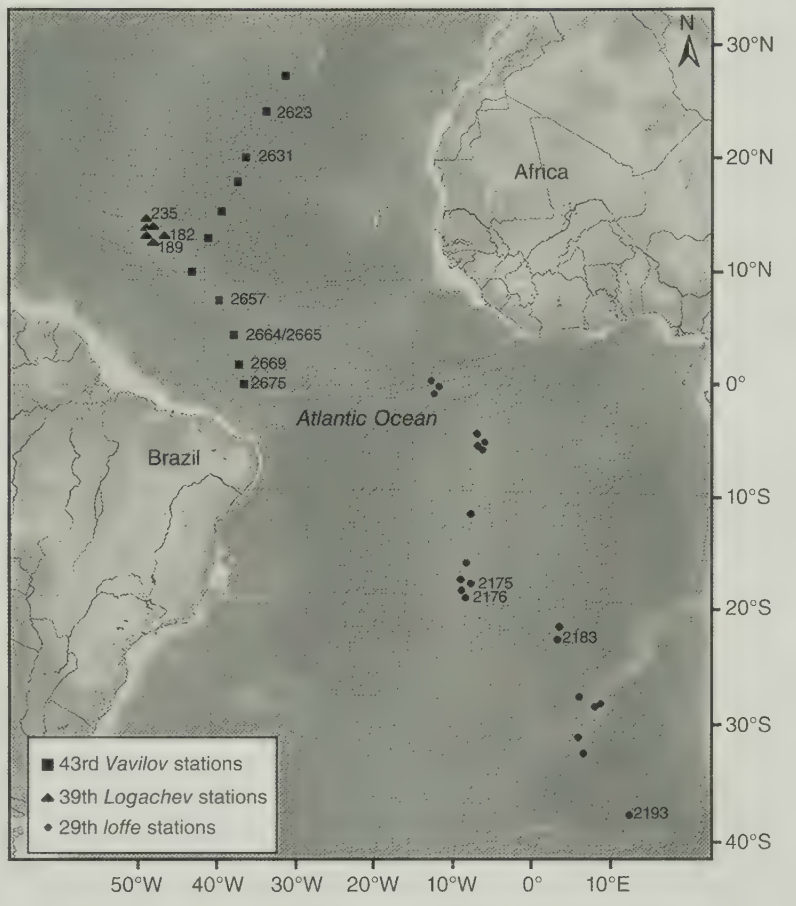

Figure 1

Map of the study area showing the locations of the all the stations sampled during the 43rd expedition of the RV *Akademik Vavilov*, 39th expedition of the RV *Professor Logachev*, and 29th expedition of the RV *Akademik Ioffe* across the Atlantic Ocean. A representative faunistic collection of ichthyoplankton and adult fish was taken during the expeditions of the RV *Vavilov* and of the RV *Professor Logachev* from the equator to latitude 30°N in 2016 and 2018. Larvae were also obtained for identification purposes from the collection of the expedition of the RV *Ioffe* to the central and South Atlantic Ocean in 2009. The numbers next to station markers are given for stations where larval lanternfish (Myctophidae) examined for this study were found. The coordinates of the stations and the dates of capture are provided in Table 1.

the Samyshev-Aseev modification. This trawl is 25 m long and has a 5-mm mesh net without nodes and with a terminal insertion of 500-µm nylon mesh and a 6-m^2 mouth area. Illustrated monographs for different areas of the Atlantic Ocean were used for identification: western central (Richards, 2005), northwest (Fahay, 2007), southeast (Olivar and Fortuño, 1991), and southwest (Bonecker and de Castro, 2006). The specimens were preserved and stored in 4% formaldehyde. The larvae were stained with alizarin following the standard procedure. All illustrations given in this paper are original.

Information for the following features are included in the descriptions: standard body length (SL), head length (HL), body depth at pectoral fin base (BD), preanal length (PAL), predorsal length (PDL), snout length (SnL), horizontal diameter of the eye (ED), number of rays in dorsal fin (D), number of rays in anal fin (A), number of rays in pectoral fin (P_1), number of rays in pelvic fin (P_2), number of rays in caudal fin (C), number of branchiostegal rays (BrR), number of gill rakers on the upper and lower parts of the first gill arch (GR), number of vertebrae (V), 2nd branchiostegal photophore (Br_2), 5th pectoral photophore (PO_5), and suborbital photophore (So).

Results and discussion

Centrobranchus nigroocellatus

Description Two larvae were identified in our collections: 4.1 mm SL (station [st.] 2675), 12.2 mm SL (st. 182) (Fig. 2). D: 11, A: 16, P_1: 15, P_2: 8, C: 6+10–9+5, GR: 0, V: 38–39, BrR: 8. The early 4.1-mm-SL larva has a deep body (BD 36% SL), laterally compressed with thin caudal peduncle. The head is large (HL 35% SL), the upper profile of the head is convex, and the snout protrudes above the lower jaw (SnL 34% HL). Oval eyes have a cone-shaped appendage of choroid tissue (ED 15% HL). The jaws are long, and the angle of the mouth reaches the vertical of the eye posterior margin. The gut is relatively straight, and the anus opens behind the middle of the body (PAL 67% SL). The larva has dorsal- and ventral-fin folds. The pectoral fins are fan-shaped and large. Rays in pectoral and ventral fins have not yet been formed. Ray formation in unpaired fins has already begun: in the caudal fin, there are 5+6 main rays, the dorsal fin starts slightly behind the middle of the body (PDL 59% SL) and has 7+ rays (larva torn), and the anal fin is behind the vertical of the middle of the dorsal fin and has 16 rays formed in it. Pigmentation of the larva includes an unpaired melanophore between the forebrain and midbrain, at the posterior edge of the orbit above the otic capsules, and at the distal edge of the gill cover. There is scattered pigment on the branchiostegial rays. Paired melanophores are above the anterodorsal margin of the pectoral fin base, and a dorsolaterally located melanophore is above the middle part of the gut. Br_2 photophores in a small larva are already formed. The body proportions of the 12.2-mm-SL larva vary slightly (BD 29% SL, HL 25% SL, 36% HL, ED 19% HL, PAL 61% SL, PDL 53% SL). The ventral fin fold almost completely disappears, and the fins have a definitive number of rays. The conical

Table 1

The stations, dates, coordinates, and depth layers of the 4 expeditions during which the larval lanternfish (Myctophidae) examined for this study were caught. A representative faunistic collection of ichthyoplankton and adult fish was taken during the expeditions of the RV *Akademik Vavilov* in the cross-section between latitude 30°N and the equator in 2016 and of the RV *Professor Logachev* in the central part of the North Atlantic Ocean in 2018. Additional materials were obtained from the collections of the expeditions of the RV *Akademik Ioffe* to the central and South Atlantic Ocean and of the RV *Akademik Kurchatov* to the west Indian Ocean.

Research vessel (expedition no.)	Station no.	Date	Coordinates	Depth layer
Akademic Vavilov (43)	2623	14 October 2016	26°34′36″N, 33°55′12″W	0–200
	2631	16–17 October 2016	22°2′36″N, 35°52′12″W	0–700
	2657	24 October 2016	08°13′54″N, 38°24′0″W	0–700
	2662	25 October 2016	4°46′18″N, 37°12′18″W	0–200
	2664	25 October 2016	4°45′54″N, 37°9′18″W	0–200
	2665	25–26 October 2016	4°43′30″N, 37°8′42″W	0–700
	2669	26–27 October 2016	2°2′30″N, 36°32′12″W	0–700
	2675	27–28 October 2016	0°1′0″S, 36°1′6″W	0–700
Professor Logachev (39)	182	27 February 2018	14°37′54″N, 44°56′12″W	0–1500
	189	1 March 2018	13°52′48″N, 45°0′36″W	0–700
	235	15 March 2018	16°18′42″N, 46°41′24″W	0–700
Akademic Ioffe (29)	2175	11 November 2009	15°45′59″S, 13°13′5″W	0–225
	2176	12 November 2009	18°0′10″S, 13°21′26″W	0–350
	2183	18 November 2009	25°42′39″S, 2°21′54″W	0–250
	2193	26 November 2009	36°56′43″S, 7°19′17″E	0–550
Akademik Kurchatov (36)	3708	19 March 1983	1°3′18″N, 56°19′18″E	0–500
	3737	2 April 1983	10°35′6″S, 50°51′0″E	0–500

appendage is long and reaches the upper jaw. Pigmentation changes somewhat: the melanophores disappear above the brain, the gut, and pectoral fin. More melanophores appear on the ventrolateral margin of the orbit, behind the olfactory capsules and on the isthmus; a line occurs on the ventral surface of the liver. PO_5 photophores begin to form.

Comparative remarks Only one species of *Centrobranchus* (*C. nigroocellatus*) is found in waters of the Atlantic Ocean (Hulley, 1981; Bekker, 1983). The development of this species in the Pacific Ocean has been described in detail (Pertseva-Ostroumova, 1964; Moser and Ahlstrom, 1970, 1996). Our 4.1-mm-SL larva has a greater body height and a larger head compared with similarly sized larvae (6.1 mm SL) from California (BD 36% SL vs. 23%, HL 35% SL vs. 27–30%). In addition, larvae from the Pacific Ocean have a later start to the formation of rays in the C, D, and A (with SL about 5 mm). There are also differences in the pigmentation of the larvae from California: at SL<5 mm, they have melanophores at the tips of both jaws, at the terminal gut section, and at the olfactory lobes of the brain, melanophores that are absent in our early larva. The pigmentation and proportion features of the 12.2-mm-SL larva correspond to those observed for larvae of a similar size from the Pacific Ocean. Although our larvae have some differences from those described in earlier reports, these differences apparently are due to the geographical variability of the species.

Bolinichthys supralateralis

Description Six larvae were collected: 4.6 mm SL (st. 2664), 8.2 mm SL (st. 2669), 10.5 mm SL (st. 2664), 11.5 mm SL, 11.5-mm SL, 11.9 mm SL (st. 189) (Fig. 3). D: 12, A: 14, P_1: 14, P_2: 8, C: 5+9–10+5, GR: (6)5+1+14(15)=20–22, V: 33–34, BrR: 9. The 4.6-mm-SL early larva is relatively deep-bodied (BD 22% SL), the head is relatively large (HL 30% SL), and the eyes are round and very large (ED 41% HL). The snout is rather blunt and short (SnL 26% HL), and the jaws almost reach the vertical of the posterior margin of the eye. There are teeth on both jaws. The intestine is wide and relatively straight, and the anus opens behind the middle of the body. The pectoral fins are large, and the rays in it are not yet formed. The dorsal fin originates in the middle of the body (PDL 50% SL), and the anal fin starts under the end of the dorsal fin (PAL 63% SL). Rays in the fins are not yet formed: in the dorsal and anal fins, pterygiophores are observed, and in the caudal fin there are rays only in the epaxial lobe. The larva is

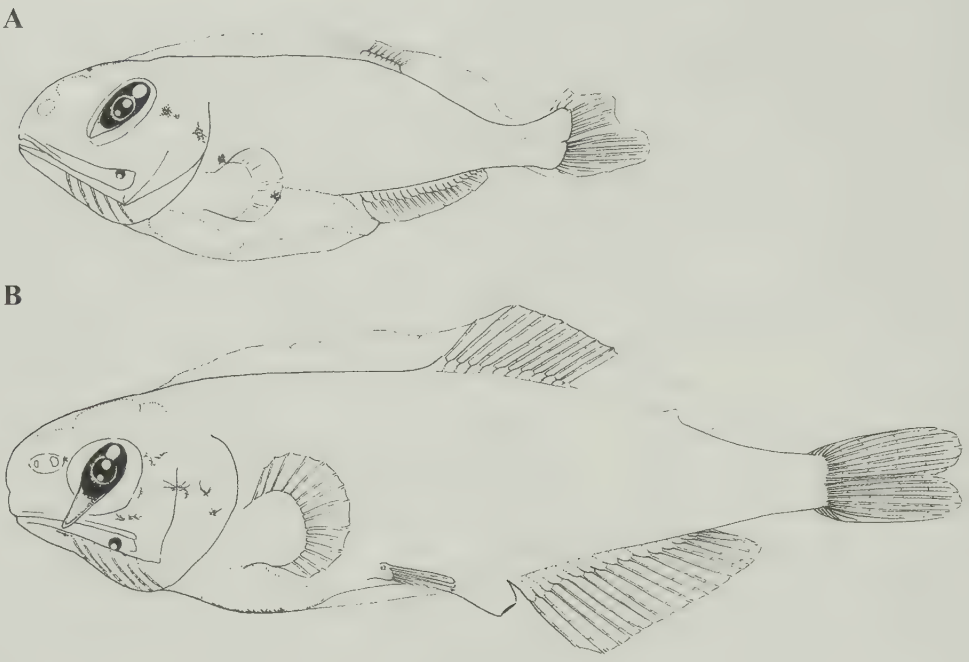

Figure 2

Illustrations of 2 early developmental stages of larval roundnose lanternfish (*Centrobranchus nigroocellatus*) caught in the central North Atlantic Ocean (**A**) at station 2675 in 2016 (4.1 mm standard body length [SL]) and (**B**) at station 182 in 2018 (12.2 mm SL).

poorly pigmented: there are paired small melanophores above the midbrain, and the internal pigment is located at the level of the otic capsule, above the gas bladder and above the terminal gut section. There are no photophores in the 4.6-mm-SL larva. With an increase in the size of larvae, the height of the body and the anteanal distance slightly increase. Otherwise, the proportions are preserved (BD 27% SL, HL 30% SL, ED 39% HL, SnL 26% HL, PAL 67% SL, PDL 50% SL). Pigmentation of the larvae persists. Melanophores located above the midbrain posterior margin enlarge and merge to form a band. Br_2 photophores are formed.

Comparative notes The larvae of *B. distofax*, *B. longipes*, *B. pyrsobolus*, and some *Bolinichthys* spp. have been described (Pertseva-Ostroumova, 1964; Moser and Ahlstrom, 1972, 1996; Olivar et al., 1999). Only 7 species of the genus are known: *B. distofax*, *B. indicus*, *B. photothorax*, *B. supralateralis*, *B. longipes*, *B. nikolayi*, and *B. pyrsobolus* (Hulley and Duhamel, 2009). The last 3 species are not found in the Atlantic Ocean. Of the 4 species living in the investigated area, the species most similar to specimens from our sampling are *B. photothorax* and *B. supralateralis*, according to the number of gill rakers (19–23); in contrast, the remaining 2 species (*B. distofax* and *B. indicus*) have ≤18 rakers. Larvae of a similar size and similar in pigmentation to our specimens are described from the Agulhas Current, which forms the western boundary current of the southern Indian Ocean, as *Bolinichthys* spp. (Olivar et al., 1999). Olivar et al. (1999) suggest that their larvae may belong to 1 of 2 species: *B. indicus* or *B. supralateralis*, which inhabit waters off the eastern coast of southern Africa. We excluded *B. photothorax* because this species does not occur in the Indian Ocean south of latitude 30°S, specifically not in the Agulhas Current (Bekker, 1983; Hulley and Duhamel, 2009). The larvae from waters of the southeast Pacific Ocean identified as *B. pyrsobolus* (Pertseva-Ostroumova, 1964) are practically no different from our larvae, but this species does not inhabit the Atlantic Ocean. On the basis of the foregoing, we preliminarily identified our larvae as *B. supralateralis*.

Diaphus sp. 1

Description Two larvae were identified in our sampling: 3.6 mm SL (st. 2665), 5.7 mm SL (st. 2665) (Fig. 4). D: 15?, A: 16, P_1: 9+, P_2: 6+, C: 6+10–9+5, GR: 10+, V: 37, BrR: 8. Larvae are relatively deep-bodied and short (BD 21–29% SL), with a relatively large head (HL 33–34% SL). The gut is fairly slender, and the anus opens slightly behind the midbody (PAL 56–63% SL); dorsal fin begins in the middle of the body (PDL 49–50% SL). The eyes are slightly oval and become round with an increase in the length of the larva (ED 31–36% HL). One melanophore is situated anteriorly on the ventral gut margin at

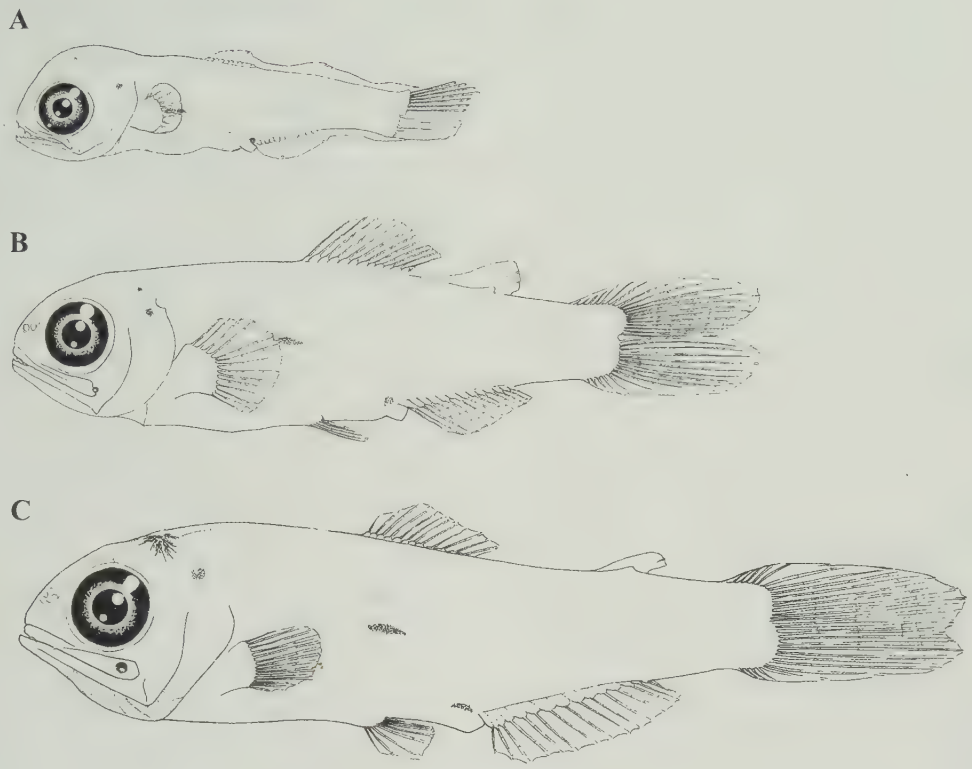

Figure 3

Illustrations of 3 early developmental stages of larval stubby lanternfish (*Bolinichthys supralateralis*) caught in the central North Atlantic Ocean in 2016 (**A**) at station 2664 (4.6 mm standard body length [SL]), (**B**) at station 2669 (8.2 mm SL), and (**C**) at station 2664 (10.5 mm SL).

Figure 4

Illustrations of 2 early developmental stages of larval *Diaphus* sp. 1 caught in the central North Atlantic Ocean in 2016 at station 2665: (**A**) 3.6 mm standard body length (SL) and (**B**) 5.7 mm SL.

the pectoral fin level; a pair are located dorsally on the terminal gut section and posteriorly to the anal fin base end, and one is on the cleithrum. Inner melanophores are noticeable above the otic capsule and above the gas bladder. With increased size of the larva, melanophores above the gas bladder spread to myosepta and a vertical row of the caudal fin rays, typical of the genus, is added. The 5.7-mm-SL larva has a Br_2 photophore symmetrically on both sides of its body.

Comparative remarks The described larvae belong to the moderately deep-bodied *Diaphus* larval type (Moser et al., 1984). In larvae of this morphotype, So photophores do not form in adults. At least 11 species of *Diaphus* without So photophores inhabit the equatorial Atlantic Ocean (Hulley, 1981), and only one of these species—*D. metapoclampus*—has a larval description (Sparta, 1952). Larvae similar to our specimens have been described by Moser and Watson (2001) as *Diaphus* sp., with the differences being in the presence of a melanophore on each side of midgut in early larvae and in the lack of melanophores on myosepta. Similar larvae also have been described by Ozawa (1986) as *Diaphus* sp. 11. The identification of all known *Diaphus* larvae is based on a serial method that uses the location of photophores in juveniles. However, early larvae with similar morphology, pigmentation, and meristic characters may turn out to be a complex of species that are almost impossible to distinguish because of the lack of photophores (Ozawa, 1986; Olivar and Beckley, 1997). Therefore, we identified these larvae only to the genus.

Nannobrachium sp. 1

Description Two larvae were identified in our collections: 4.0 mm SL (st. 2662), 8.0 mm SL (st. 2183) (Fig. 5). D: 13, A: 17, P_1: 13, P_2: 8, C: 5+9–9+5, GR: 10+, BrR: 8. The 4.0-mm-SL larva has a deep body (BD 39% SL). The head is large, taking almost half of the body length (HL 44% SL), with an elongated, pointed rostrum (SnL 37% HL). Eyes are round (ED 33% HL). The jaws are long and end behind the vertical of the eye middle. The pectoral fins are fan-shaped. The gut is wide and relatively straight, and the anus opens far behind the midbody (PAL 73% SL). The dorsal fin begins slightly behind the middle of the body (PDL 63% SL), and the anal fin begins under the end of the dorsal fin. Pigmentation of the head includes minute melanophores at the tips of the jaws, paired melanophores anterior to the midbrain, unpaired melanophores above the forebrain, and one melanophore each posterior to the midbrain and to the hindbrain. There are several melanophores on the opercle and on the cleithrum. The inner side of the pectoral fin's base and the base of the pectoral and ventral fin rays are pigmented. Internal melanophores are noticeable in the middle part of the horizontal septum, as well as on the myosepta of the oblique muscle of the

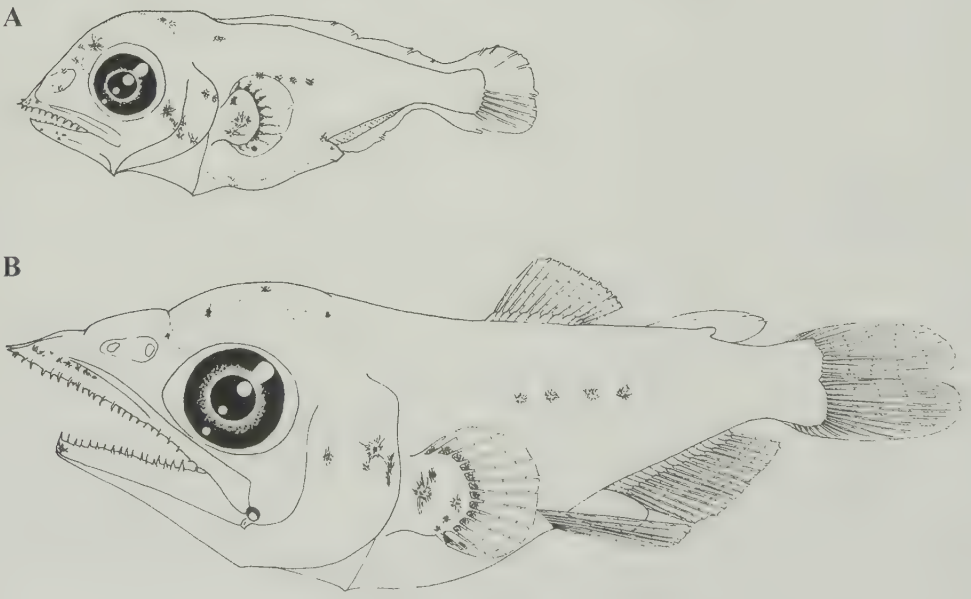

Figure 5

Illustrations of 2 early developmental stages of larval *Nannobrachium* sp. 1 caught (**A**) in the central North Atlantic Ocean in 2016 at station 2662 (4.0 mm standard body length [SL]) and (**B**) in the Walvis Ridge region in the South Atlantic Ocean in 2009 at station 2183 (8.0 mm SL) (redrawn).

abdomen. Br_2 photophores are not yet formed. Morphology of the 8.0-mm-SL larva has been described earlier (we previously identified this specimen as *Nannobrachium wisneri* in Bolshakova and Evseenko, 2016, by counting characters and considering the place of capture). In general, the pigmentation pattern has not changed. Body depth, eye diameter, and predorsal length are decreased; anteanal and snout length are increased (BD 31% SL, HL 45% SL, SnL 45% HL, ED 24% HL, PAL 78% SL, PDL 58% SL). There are Br_2 photophores.

Comparative remarks There are several opinions about phylogenetic relationships within the genus *Lampanyctus*. One opinion is that the genus *Nannobrachium* is a junior synonym of *Lampanyctus*; other authors recognize its validity (Bekker, 1983; Moser and Ahlstrom, 1996; Olivar and Beckley, 1997; Zahuranec, 2000). According to the latest information (Kobyliansky, 2016), there are no osteological differences between groups within the genus *Lampanyctus*, confirming the opinion of monophyly of this genus. In spite of this notion of monophyly, here, we use the names *Nannobrachium* and *Lampanyctus* following Moser and Ahlstrom (1996) to designate larvae with a rostrum that is long and short, respectively.

On the basis of a number of characters, including elongated jaws, long rostrum, large head, large pectoral fins, and posteriorly displaced dorsal fin (Moser et al., 1984; Zahuranec, 2000), we assign these larvae to the genus *Nannobrachium*. A series of similar larvae of different sizes from the Pacific Ocean and from the tropical and subtropical Atlantic Ocean have been described (Ozawa, 1986; Moser and Watson, 2001). Our larvae differ from larvae collected in the Pacific Ocean only in the presence of a pigment row on the isthmus and anterior to the anus; our specimens have no differences from the larvae from the Atlantic Ocean. Moser and Watson (2001) suggest that a larva such as our specimens belongs to a species found in the Atlantic Ocean that is close to *N. nigrum*. Note that Zahuranec (2000), on the basis of adult characters, identified 5 phylogenetic groups within the genus *Nannobrachium*: the Nigrum, Regale, Cuprarium, Achirus, and Isaacsi species groups. Moser et al. (1984) also identified several groups according to larval characters: *L. regalis-L. ater* (*L. regalis* and *L. ater* are now considered synonyms of *N. regale* and *N. atrum*, respectively), *L. lineatus-L. cuprarius* (*L. lineatus* and *L. cuprarius* are now considered synonyms of *N. lineatum* and *N. cuprarium*, repectively), and *L. achirus* (now considered a synonym of *N. achirus*). The group *L. lineatus-L. cuprarius* is fully consistent with the species composition of the Cuprarium group described by Zahuranec (2000). The larvae of *N. nigrum* and *N. atrum* (Richards, 2005) have preopercular spines that are absent in other known larvae, and Zahuranec (2000) placed adults of both of these species in the Nigrum group. The morphotype of the larva that we are describing is characterized by the absence of preopercular spines.

We compared the pigmentation and plastic characters of our larvae with the larval characters used by Olivar and Beckley (1997) to construct a similarity matrix for the *Lampanyctus* larvae. The results of a comparison of characters indicate that our larva was closest to *N. regale*. The similarity is noticeable in 22 of 24 features, except for pigmentation on the dorsal tail and eye size. Therefore, we believe that they are the larvae of a species not yet described and that that they inhabit the tropical and subtropical Atlantic Ocean and, possibly, the western Pacific Ocean. Despite the existing correspondence between the groups established on the basis of larval and adult characters, the Regale group still has an important inconsistency: in the larvae of *N. ritteri* and *N. idostigma*, the jaws are not elongated, as they are in the larvae of other *Nannobrachium* species. The small number of species for which larvae of the genus *Lampanyctus* have been described prevents correlation between adult and larval groups of this genus.

Lampanyctus vadulus

Description A single larva was collected: 7.5 mm SL (st. 2657) (Fig. 6B). D: 14, A: 18, P_1: 12, P_2: 5+, C: 3+9–10+4, GR: 4+1+9=14, V: 36–37, BrR: 8. The larva has a deep body (BD 37% SL) and a large head (HL 40% SL) with long jaws extending beyond the vertical of the eye posterior margin. The snout is rather long (SnL 33% HL), and the eye is round (ED 27% HL). Anus opens slightly behind the middle of the body. The dorsal fin begins about the middle of the body (PDL 55% SL) and has 14 rays. The anal fin starts under the 5–6 ray of the dorsal fin (PAL 62% SL) and has 18 rays. The larva has several pigment spots at the upper and lower jaw tips, an unpaired melanophore above the forebrain, and large paired melanophores located posterolaterally to the midbrain. There is an internal melanophore anterior the dorsal fin base and a large unpaired melanophore located dorsally under the middle of the adipose fin base. Paired large melanophores are present on the dorsal side of the terminal gut section; the inner pigment is above the gas bladder. The pigment on the anterial side of the liver forms a strip.

Comparative remarks Habitually, the larva from our sampling is similar to the larvae of the genus *Lampanyctus* (for differences, see the "Comparative remarks" section for *Nannobrachium* sp. 1). Illustrated descriptions of similar larvae designated as *Lampanyctus* sp. 7 have been made for larvae from the western Pacific Ocean (Ozawa, 1986). In addition, in the IO RAS collections (5.5-mm-SL larva from st. 3737 and 2 larvae [5.4 and 5.5 mm SL] from st. 3708 of the 36th cruise of the RV *Kurchatov*) taken in the Indian Ocean's equatorial part, we found larvae like our specimens (Fig. 6A). All of these larvae are identical, both in pigmentation and in meristic features (proportions of larvae from the Indian Ocean: BD 35% SL, HL 38% SL, SnL 39% HL, ED 32% HL, SAL 63% SL, PDL 56% SL); our 7.5-mm-SL larva differs only in the presence of a pigment series on the isthmus. According to Hulley (1981), Bekker (1983), and Wisner (1976), not a single known species of *Lampanyctus* inhabits the western Pacific Ocean, tropical Atlantic Ocean, or Indian Ocean. Among species whose

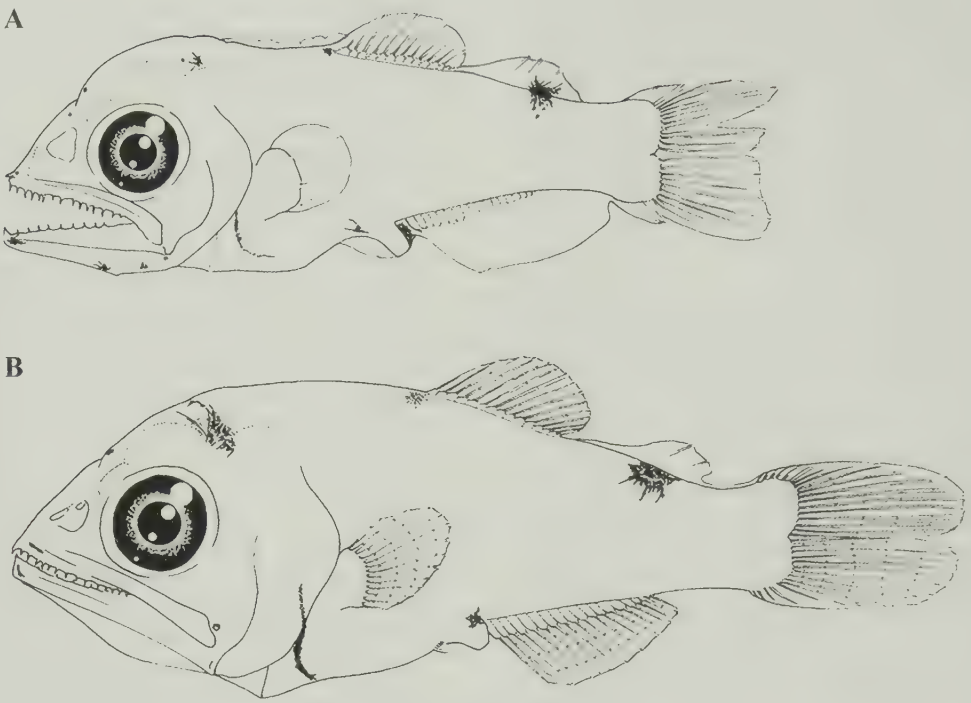

Figure 6

Illustrations of 2 early developmental stages of larval noble lanternfish (*Lampanyctus vadulus*) caught (**A**) in the Indian Ocean in 1983 at station 3737 (5.5 mm standard body length [SL]) and (**B**) in the central North Atlantic Ocean in 2016 at station 2657 (7.5 mm SL).

larvae are not described, only *L. macropterus*, which lives in the equatorial waters of the Pacific and Indian Oceans, has similar meristic characters (D: 13–15, A: 18–19, P_1: 13–15; GR: 13–15), and *L. vadulus* is the only one among the species in the Atlantic Ocean to have a central distribution type (Hulley, 1981; Bekker, 1983). Therefore, we preliminarily identify this larva as *L. vadulus*.

Lampanyctus sp. 1

Description Ten larvae were found in our collections: 8.0 mm SL (st. 2623), 8.4 mm SL (st. 2631), 8.7 mm SL (st. 235), 6.6 mm SL (st. 2175), 3.2 mm SL (st. 2176), 5.5, 6.4, 6.9, 8.5 mm SL (st. 2183), 10.0 mm SL (st. 2193) (Fig. 7). D: 14, A: 17, P_1: 13–14, P_2: 8, C: 6+10–11+5, GR: 4+1+9–10, V: 33–34, BrR: 8. Larvae are deep-bodied (BD 33–36% SL) with a large head (HL 30–36% SL). The anus opens behind the middle of the body (PAL 65–66% SL). Eyes are round and large (ED 34–39% HL). The snout is pointed (SnL 26% HL); in large larvae, the jaws reach the vertical of the eye posterior margin; and there are prominent teeth on both jaws with an anterior tooth patch on the upper one. The gut is relatively straight. The dorsal fin originates near the midbody (PDL 54–57% SL). All the rays in fins are distinguishable in the 8.4-mm-SL larva. Pigmentation consists of paired melanophores anterior to the midbrain and posterior to the hindbrain (SL >6.6 mm), 1 melanophore situated on the opercle and several on the cleithrum, 2–3 melanophores on the base of the pectoral fin, and 1 or more melanophores on the tips of jaws. Inner melanophores above the gas bladder are visible. With an increase in the size of the larvae, melanophores are added at myosepta between the pectoral and pelvic fins. Br_2 photophores are already noticeable on the 6.4-mm-SL larva.

Comparative remarks Larvae were found in the subtropical zones of both the North and South Atlantic Ocean. Among the species in the Atlantic Ocean with this type of distribution, *L. tenuiformis* and *L. photonotus* are similar by the complex of meristic characters. However, the early stages of development of these species are known (Moser and Ahlstrom, 1996; Moser and Watson, 2001) and differ from those of our larvae in pigmentation especially. On the basis of the features applied by Olivar and Beckley (1997) to separate *Lampanyctus* larvae into groups, our larvae are closest to the second group, which includes *L. parvicauda*, *L. idostigma*, *L. nobilis*, *L. ritteri*, the jewel lanternfish (*L. crocodilus*), and *L. australis*, among others, but the larvae differ in pigmentation pattern from larvae of all known *Lampanyctus* species. Perhaps these larvae belong to a species not yet described.

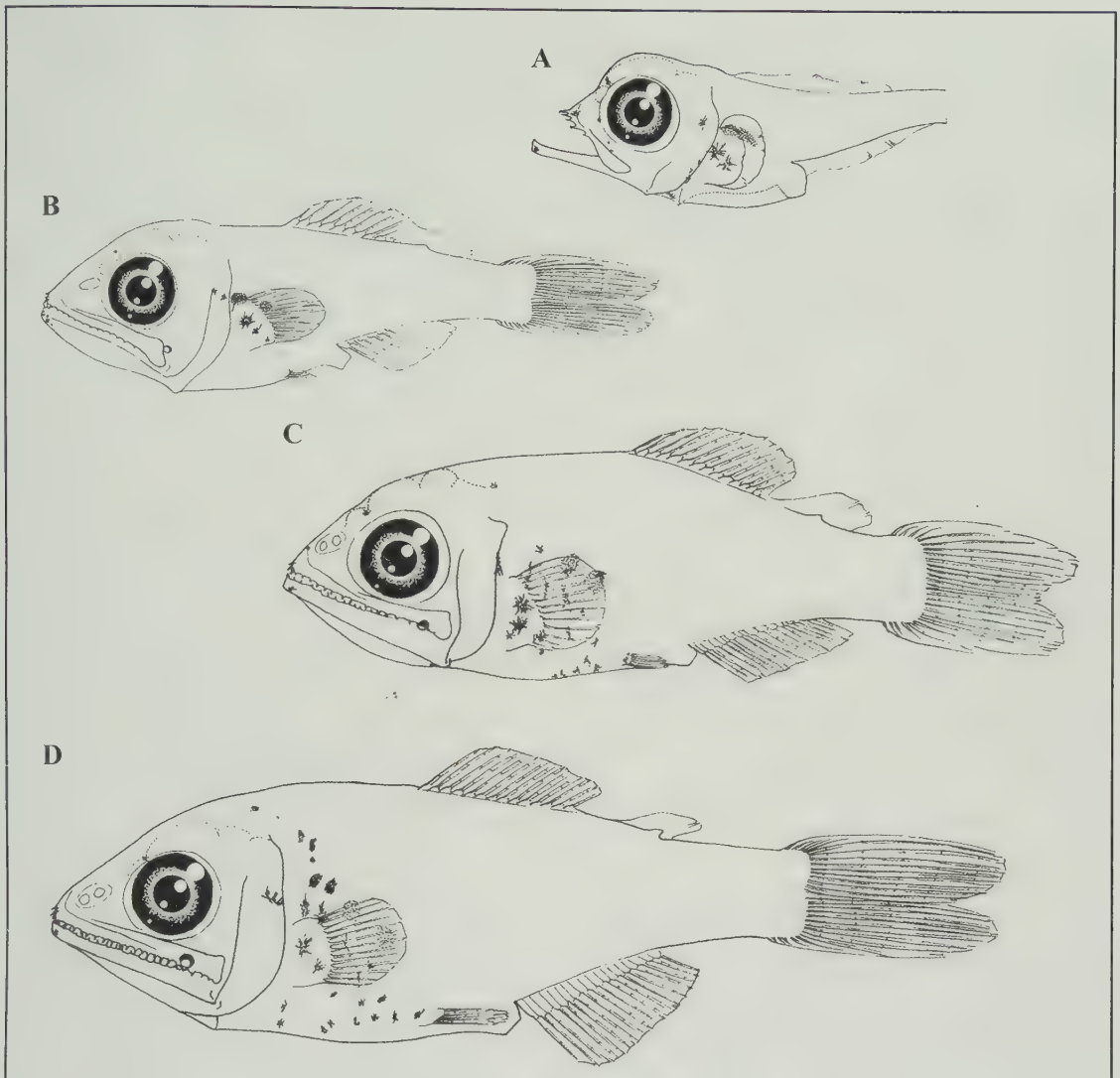

Figure 7

Illustrations of 4 developmental stages of larval *Lampanyctus* sp. 1 caught in the central South Atlantic Ocean in 2009 (**A**) at station 2176 (3.2 mm standard body length [SL]) and (**B**) at station 2175 (6.6 mm SL), (**C**) in the central North Atlantic Ocean in 2016 at station 2631 (8.4 mm SL), and (**D**) in the Walvis Ridge region in the South Atlantic Ocean in 2009 at station 2193 (10.0 mm SL).

Acknowledgments

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Abundance and distribution of Atlantic cod (*Gadus morhua*) in a warming southern New England

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Abstract—Atlantic cod (*Gadus morhua*) in southern New England (SNE) and along the mid-Atlantic coast have been described as the world's southernmost population of this species, but little is known of their population dynamics. Despite the expectation that SNE Atlantic cod are or will be negatively influenced by increasing water temperatures due to climate change, fisheries that target Atlantic cod in this region have reported increased landings during the past 2 decades. The work described here used ichthyoplankton and trawl survey data to investigate spatial and temporal patterns of abundance of Atlantic cod, and their potential links to environmental factors, across multiple life stages in Rhode Island. The results identify waters of the state of Rhode Island as a settlement and nursery area for early stages of Atlantic cod until water temperatures approach 15°C in late spring. Atlantic cod that were age 1 or older used coastal habitats when water temperatures were within their documented thermal preferences. The data indicate that abundance of Atlantic cod in SNE has increased since 2000, but continued warming of winter water temperatures may limit future recruitment. The improved understanding of the life history and population dynamics of Atlantic cod in SNE provides insights into stock structure and productivity in a poorly understood and vulnerable portion of their geographic distribution.

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Atlantic cod (*Gadus morhua*) in the northwest Atlantic Ocean have historically ranged as far south as Cape Hatteras, North Carolina (Schroeder, 1930; Bigelow and Schroeder, 1953). However, because aggregations documented during the winter months off New York, New Jersey, and Rhode Island represent the southern limit of known spawning activity for this species (Smith, 1902; Wise, 1963) and no significant quantity of eggs or larvae have been found south of Long Island in recent decades (Serchuk and Wood[1]; Berrien and Sibunka, 1999), the geographic region of southern New England (SNE) is thought to have the world's southernmost indigenous population of Atlantic cod (Wise, 1958). Atlantic cod within U.S. waters are assessed and managed as 2 stocks: Georges Bank and the Gulf of Maine, with Atlantic cod in SNE included in the Georges Bank management unit (Zemeckis et al., 2014a). Both stocks are currently in a critically depleted state (NEFSC[2,3]), but the status of Atlantic cod in SNE is poorly understood because Atlantic cod have been infrequently observed in fishery-independent trawl surveys. Consequently, survey sampling areas, or strata, in SNE are not incorporated

[1] Serchuk, F. M, and P. W. Wood. 1979. Review and status of the southern New England–Middle Atlantic cod, *Gadus morhua*, populations. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., Woods Hole Lab. Ref. Doc. 79-37, 77 p. [Available from Woods Hole Lab., Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., 166 Water St., Woods Hole, MA 02543.]

[2] NEFSC (Northeast Fisheries Science Center). 2017. Georges Bank Atlantic cod. *In* Operational assessment of 19 Northeast groundfish stocks, updated through 2016. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 17-17, p. 38–46. [Available from website.]

[3] NEFSC (Northeast Fisheries Science Center). 2017. Gulf of Maine Atlantic cod. *In* Operational assessment of 19 Northeast groundfish stocks, updated through 2016. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 17-17, p. 26–37. [Available from website.]

in the stock assessment for the Georges Bank management unit of Atlantic cod (NEFSC, 2013). Although the region has not sustained biomass levels as high as other waters of the United States, Atlantic cod in SNE have historically supported significant recreational and commercial fisheries that have made important economic contributions to coastal communities (Serchuk and Wood[1]; Oviatt et al., 2003).

Results of past research provide some insights into population dynamics of Atlantic cod in SNE. Findings from tagging experiments indicate that SNE Atlantic cod may represent a separate spawning group that significantly mixes with cod inhabiting the Nantucket Shoals region but that exhibits very limited movements to the stock area in the Gulf of Maine (Schroeder, 1930; Wise, 1958; Tallack, 2011). The results of these efforts indicate that Atlantic cod south of Cape Cod, Massachusetts, may represent 2 distinct spawning groups: 1 group south of Massachusetts and Rhode Island in SNE and 1 group off the coast of New Jersey (Smith, 1902). These groups are thought to use similar habitats around the Great South Channel and Nantucket Shoals during the summer months (Wise, 1963; Serchuk and Wigley, 1992). Peak spawning of Atlantic cod in the SNE region has historically occurred during the winter, on the basis of collections of fish in spawning condition (Wise, 1958; Serchuck and Wood[1]) and eggs or larvae of Atlantic cod in ichthyoplankton tows (Berrien and Sibunka, 1999), and the peak in spawning has overlapped with a peak in commercial fishing effort (Serchuk and Wood[1]). More contemporary winter–spring observations of spawning Atlantic cod collected from waters south of Rhode Island indicate that this spawning seasonality has remained stable (Loehrke, 2013).

Although spawning in SNE is well-documented, the connectivity among Atlantic cod in SNE and in other regions is uncertain. Results from larval modeling studies indicate that Atlantic cod eggs or larvae spawned within the western Gulf of Maine (i.e., near Ipswich Bay, Massachusetts, or in Cape Cod Bay) may reach SNE prior to settlement (Huret et al., 2007; Churchill et al., 2011). Meanwhile, findings from other dispersal studies indicate that larvae spawned on the northeastern peak of Georges Bank largely remained near their spawning sites with little transport to SNE (Lough et al., 2006). In agreement with these results, findings from genetic analyses indicate that Atlantic cod in SNE are more closely related to winter-spawning Atlantic cod from the Gulf of Maine than to Atlantic cod spawning on eastern Georges Bank (Wirgin et al., 2007; Kovach et al., 2010). Although genetic results indicate that some connectivity exists, it is likely that the larval transport contribution of the Gulf of Maine to SNE may be minor or negligible. Furthermore, the role of physical transport (i.e., wind) in spawner–recruit dynamics of Atlantic cod has been shown to be less robust than previously proposed, indicating that physical oceanography may be less of a factor in recruitment and stock abundance of this species (Hare et al., 2015). Given documentation of local spawning in SNE, these lines of evidence have been used to theorize whether or not Atlantic cod in this region should be considered self-sustaining (Zemeckis et al., 2014a).

The SNE region is relatively shallow and warm when compared with other areas inhabited by Atlantic cod (ICES, 2005). As a result, productivity of Atlantic cod in this region has been expected to decline because of anticipated adverse effects of climate change on their life history, including decreased recruitment, increased competition, reduced available thermal habitat, and increased metabolic costs (Drinkwater, 2005; Fogarty et al., 2008). Atlantic cod on Georges Bank are thought to have a high climate exposure and high potential for distributional change (Hare et al., 2016) and are therefore expected to shift their distribution and center of biomass northward (Drinkwater, 2005; Kleisner et al., 2017; Selden et al., 2018), potentially resulting in the extirpation of Atlantic cod from SNE. Nye et al. (2009) found that the center of biomass of the Georges Bank stock of Atlantic cod had already shifted poleward by an average of 1.48 km/year and that the area it occupied had decreased by an average of 454.5 km^2/year between 1968 and 2007. In contrast to these expectations, however, accounts from recreational anglers indicate that abundance of Atlantic cod in waters south of Rhode Island has significantly increased during the past 15 years (Sheriff, 2018). If true, such an increase would indicate that the adverse effects of climate change on Atlantic cod in SNE, and perhaps elsewhere, may be less severe or more complex than has been previously hypothesized.

The aim of the work described here was to analyze existing data sets to provide a better understanding of the distribution and habitat utilization of Atlantic cod in the most southern portion of their geographic range. Several fishery-independent surveys and fishery-dependent data sources capturing multiple life stages (i.e., larva, young of the year [YOY], juvenile, and adult) of Atlantic cod from Rhode Island, which is at the center of the SNE region, were investigated to address 3 objectives: 1) provide a contemporary description of the distribution of Atlantic cod in SNE waters, 2) evaluate trends in relative abundance, and 3) determine if recent trends in abundance in SNE appear to have any significant relationship with habitat characteristics or environmental conditions (e.g., temperature).

Materials and methods

Larval surveys

Data on the abundance of larval Atlantic cod were available from ichthyoplankton surveys conducted by the Rhode Island Department of Environmental Management (RIDEM) during 2001–2008 and later renewed by RIDEM and the University of Rhode Island Graduate School of Oceanography (URIGSO) during 2016–2017. For the RIDEM survey in 2001–2008, tows of 335-μm plankton

nets for 6 min at 15 stations within Narragansett Bay (Fig. 1, A and B) were performed biweekly throughout each year. The collected samples were identified to the species level, and their densities were reported as number per 100 cubic meters. For the RIDEM and URIGSO survey in 2016–2017, the methods of the earlier study were followed closely, and 6-min tows of 335-µm plankton nets were performed weekly at 15 stations within Narragansett Bay between February and April.

In both surveys, the nets were towed for 2 min each near the bottom, at half the bottom depth, and at the surface for stations located at depths ≥11 m and were towed for 3 min each near the bottom and at the surface for stations located at depths <11 m. During tows, date, location, depth, and water temperatures at the surface and bottom were recorded. Fourteen of the stations sampled during the survey in 2016–2017 matched those sampled in 2001–2008, with 1 station relocated from the

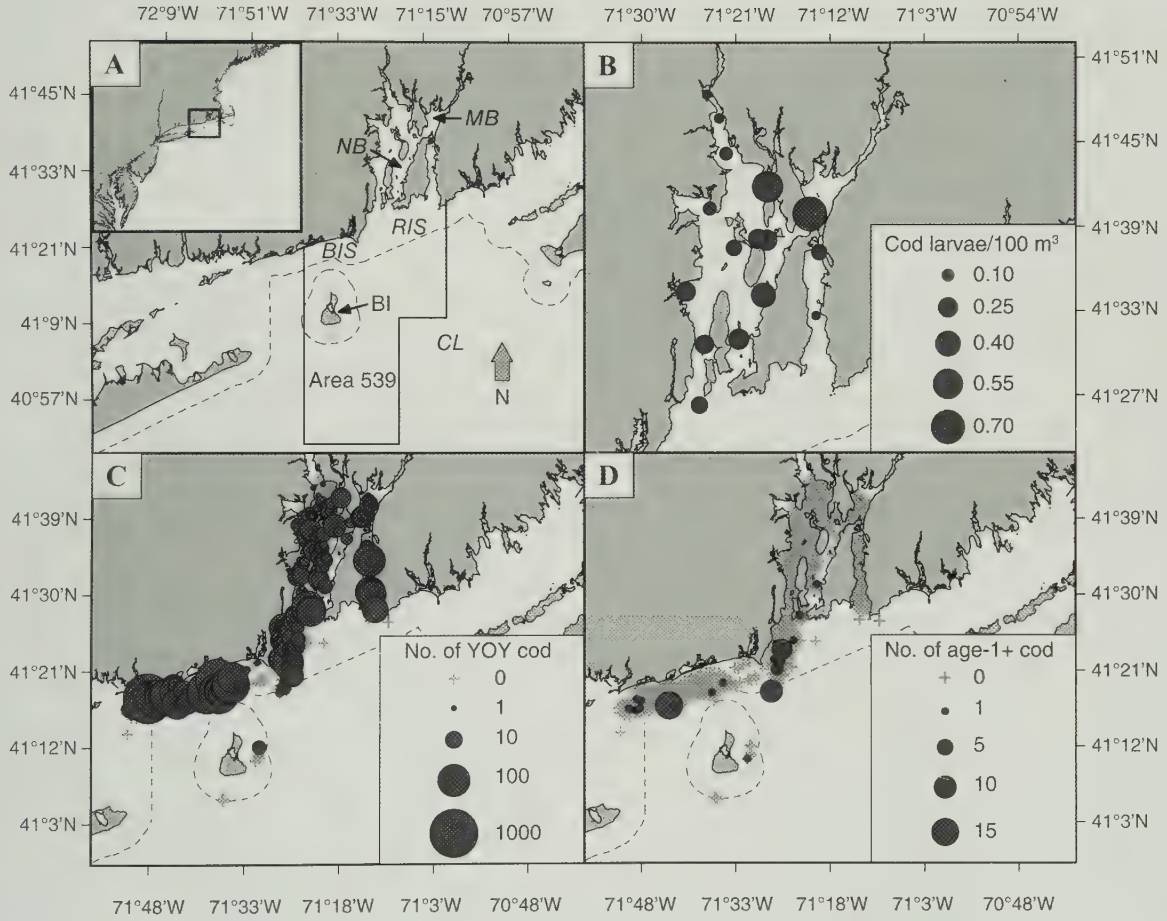

Figure 1

(**A**) A map of nearshore waters in Rhode Island where Atlantic cod (*Gadus morhua*) were sampled, and maps showing abundance of (**B**) larval and (**C**) young-of-the-year (YOY) Atlantic cod and (**D**) those age 1 or older (age 1+). The dashed black lines depict the limit of state waters for Rhode Island and neighboring states, and the black line in panel A indicates the boundaries of NOAA statistical area 539. In panel B, abundance from ichthyoplankton surveys conducted in 2001–2008 and 2016–2017 is presented as the mean measured density (number of larvae/100 m^3) for the time series by location, with circle size depicting differences in density between locations. In panels C and D, values of abundance for YOY and age-1+ Atlantic cod are from trawl surveys conducted in 1979–2018 by the Rhode Island Department of Environmental Management. Abundance of YOY Atlantic cod is presented as total counts for the time series by location, with circle size proportional to log-abundance and plus signs representing tows in which no Atlantic cod were caught. Abundance of age-1+ cod is presented as total counts for the time series by location, with circle size proportional to abundance and plus signs representing trawls in which no Atlantic cod were caught. The following locations are designated: Narragansett Bay (NB), Mount Hope Bay (MB), Rhode Island Sound (RIS), Block Island Sound (BIS), Block Island (BI), and Cox Ledge (CL).

mouth of Narragansett Bay to Mount Hope Bay in the northeastern portion of the estuary (Fig. 1A). The samples collected as part of this survey were then preserved in 5% buffered formalin and returned to the lab where larval cod were identified, counted, and measured. Data were collected on the volume sampled during each tow by using Sea-Gear Mechanical Flowmeters (Sea-Gear Corp., Melbourne, FL), and larval densities were calculated for comparisons among years. Differences in the size distributions and temperature conditions in 2016 and 2017 were evaluated with Wilcoxon rank-sum tests because of non-normality. Additionally, ages were approximated by using the average linear and exponential growth curves reported by Green et al. (2004) and by assuming a mean egg stage duration of 18 d (Fahay et al., 1999) in order to estimate the spawning season. A 2-sample Kolmogorov–Smirnov test was used to test for agreement in the distributions of estimated spawning dates between years. All statistical analyses were conducted in R, vers. 3.5.1 (R Core Team, 2018).

Trawl surveys and landings data

Data on abundance of Atlantic cod were analyzed from the URIGSO weekly trawl survey and the RIDEM trawl survey. The URIGSO trawl survey has been (1959–present) conducted at 2 stations in Narragansett Bay: a mid-bay habitat with a mean depth of ~7 m and an outer-bay habitat with a mean depth of ~23 m (Collie et al., 2008). For this survey, an otter trawl net with 7.6-cm mesh shrinking to 5.1 cm in the codend and an effective opening of 6.5 m is towed at a speed of 1.03 m/s (2 kt) for 30 min. Counts and, beginning in 1994, aggregate weights have been recorded for each species upon retrieval of every tow. The RIDEM survey has been conducted as 3 distinct components varying spatiotemporally. The monthly survey (1990–present) is conducted at 13 fixed stations in Narragansett Bay, with each station being sampled once a month throughout the year. The spring and fall (seasonal) surveys (1979–present) include the same fixed stations of the monthly survey and additional fixed and randomly chosen stations in Narragansett Bay, Rhode Island Sound, and Block Island Sound (Fig. 1, A, C, and D). The spring survey traditionally operates between mid-April and mid-May, and the fall survey is conducted from mid-September through early October. For these trawl surveys, an otter trawl net with a 6.7-m effective opening and a 0.6-cm mesh liner in the codend is towed at a speed of 1.29 m/s (2.5 kt) for 20 min. The total catch is weighed, and all fish are measured for total length (TL).

Atlantic cod captured in the RIDEM trawl survey were separated into approximate age classes based on TL for the purpose of analysis. Size thresholds of 20 and 37 cm TL were used to differentiate YOY Atlantic cod from juveniles (NEFSC, 2013) and juveniles from adults (Serchuk and Wood[1]; NEFSC, 2013), respectively, on the basis of the average size at age of 1- and 2-year-old Atlantic cod reported in the stock assessment for the Georges Bank management unit. Because YOY Atlantic cod were observed in many months, descriptive statistics for observations of this life stage were calculated by using only the RIDEM monthly survey component to avoid bias from the temporal constraints of the seasonal trawl surveys. Juvenile and adult Atlantic cod were observed infrequently in the RIDEM trawl survey and were most often caught in areas sampled only during the seasonal surveys. Therefore, all available observations of these age classes were considered in descriptive analyses. Because of the limitations of data from the URIGSO survey, only data on Atlantic cod from the RIDEM survey could be analyzed by size class. It was assumed that Atlantic cod captured in the URIGSO trawl survey were juveniles or adults on the basis of the mesh size of the net. During tows, date, location, depth, and bottom water temperature were recorded as part of the URIGSO and RIDEM surveys. Comparisons of the depth and temperature of capture by age class were made with Wilcoxon rank-sum tests.

To assess prospective responses to observed changes in abundance by using fishery catch data, landings of Atlantic cod were obtained from the Marine Recreational Information Program (MRIP) (recreational fisheries statistics, available from website) and the vessel trip report (VTR) program of the NOAA Northeast Fisheries Science Center (NEFSC) (Ares[4]). Specifically, recreational landings of Atlantic cod by Rhode Island anglers for all waves and modes of fishing were analyzed for the period 1981–2018. The VTR data were gathered for commercial fisheries and party and charter (recreational) vessels operating in NOAA statistical area 539 (i.e., the closest spatial representation to the state waters of Rhode Island) between 2004 and 2018 (Fig. 1A). Although VTRs are not mandated for the state-permitted party and charter fleets, most of these Rhode Island businesses report their activity by using VTRs (Lake[5]). Landings data were compared with abundances of Atlantic cod in surveys of Rhode Island waters by using Pearson's product-moment correlation coefficient (r).

To gain insight into the potential causes of modern trends in observed abundance of Atlantic cod in Rhode Island state waters, the relationship between water temperature and the annual mean catch per unit of effort (CPUE) in the URIGSO and RIDEM trawl surveys was explored during the period of reported increase (2000–2018) with generalized linear models (GLMs) by using the R package mgcv, vers. 1.8-24 (Wood, 2011). Because the CPUE values are positively skewed and contain many zeros, Tweedie distributions were used to describe the errors of the regression fits. For comparison with abundance of YOY Atlantic cod and those that were age 1 or older (age 1+), monthly bottom water temperatures were obtained from the URIGSO trawl survey for the outer-bay habitat at the mouth of Narragansett Bay during 1959–2018.

[4] Ares, N. 2020. Personal commun. Rhode Island Div. Mar. Fish., 3 Fort Wetherill Rd., Jamestown, RI 02835.

[5] Lake, J. 2019. Personal commun. Rhode Island Div. Mar. Fish., 3 Fort Wetherill Rd., Jamestown, RI 02835.

Additionally, other factors that could influence the dispersal and survival of cod larvae were tested in the GLMs for YOY Atlantic cod. Monthly mean wind speed and direction and monthly precipitation accumulation (a proxy for estuarine salinity) data were accessed from the NOAA National Climatic Data Center (available from website) for the monitoring station at the Theodore Francis Green Memorial State Airport in Warwick, Rhode Island. Here, each daily vector for the direction of the fastest 2-min wind was assumed to have unit length and have decomposed into northerly and easterly components before being averaged by month. The winter index (mean for December–March) of the North Atlantic Oscillation was also obtained, from the National Weather Service Climate Prediction Center (available from website), because of the documented effect of this climate phenomenon on the winter wind field and circulation south of Rhode Island (Luo et al., 2013). Forward variable selection was performed for all GLMs with an inclusion threshold of a 2-point reduction in the Bayesian information criterion (BIC).

Results

Distribution in waters of Rhode Island

During the ichthyoplankton surveys conducted in 2001–2008 and 2016–2017, larvae and postlarvae of Atlantic cod were observed throughout Narragansett Bay between January and May, with the highest densities observed in the northeastern and southern portions of the estuary (Fig. 1B). Specimens captured in the survey in 2016–2017 (number of samples [n]=510) ranged in size between 4 and 34 mm TL (Fig. 2A). The median dates of capture were 2 April in 2016 and 23 March in 2017. Further, the median length of larvae captured in 2016 (13.2 mm TL) was significantly larger than that of larvae caught in 2017 (8.7 mm TL; Wilcoxon rank-sum test: $P<0.001$). The median surface water temperature at which larval Atlantic cod were collected was significantly warmer in 2016 (7.6°C) than in 2017 (3.9°C; Wilcoxon rank sum test: $P<0.001$). Estimated spawning dates for the collected larval Atlantic cod were between late December and mid-February (linear growth: 26 December–18 February; exponential growth: 1 January–15 February; Fig. 2B). Despite differences in larval size, time of capture, and temperature at capture, the frequency distributions of estimated spawning dates were not significantly different between collection years (Kolmogorov–Smirnov test: $P>0.05$).

Young-of-the-year Atlantic cod (n=8259) were observed throughout all of Rhode Island state waters in the RIDEM trawl survey between 1979 and 2018 (Fig. 1C). These Atlantic cod were caught across a wide depth range, with collections occurring between 2.7 and 46.0 m (95% highest density interval in the RIDEM monthly survey component: 4.6–20.4 m). The YOY Atlantic cod were captured primarily between March and June, with the vast majority being observed in April and May (Fig. 3A) and at temperatures ranging from 0.0°C to 22.3°C. The 95% highest density interval of collections in the RIDEM monthly survey component occurred between 0.0°C and 14.0°C (Fig. 3B). Although some YOY Atlantic cod were observed during the fall months in the RIDEM fall survey component (August–December: n=15), this age class

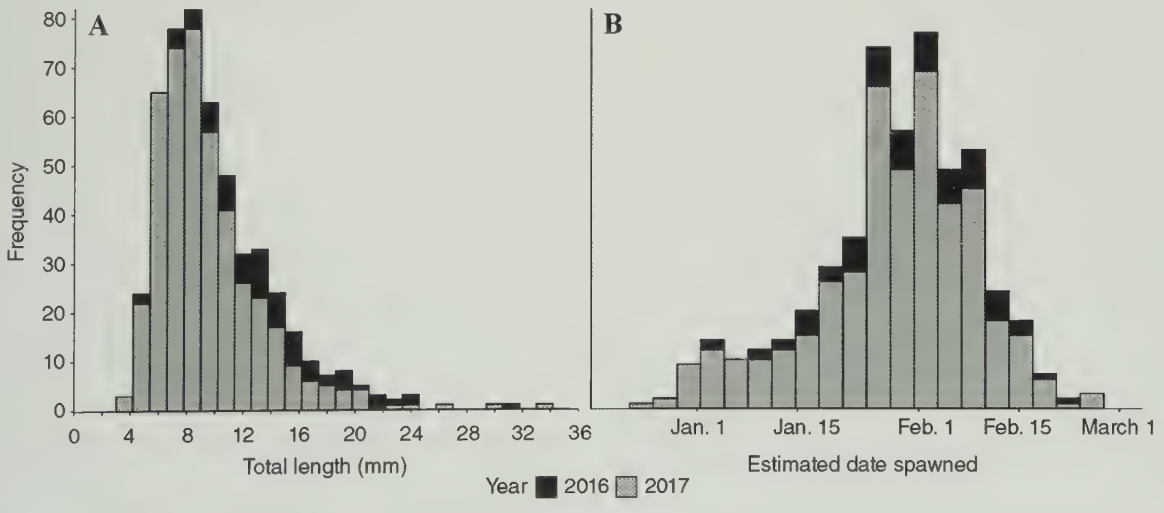

Figure 2

Frequency distributions of (**A**) total length and (**B**) estimated spawning dates of larval Atlantic cod (*Gadus morhua*) captured during ichthyoplankton surveys conducted in 2016 and 2017 by the Rhode Island Department of Environmental Management and the University of Rhode Island Graduate School of Oceanography in Narragansett Bay, Rhode Island.

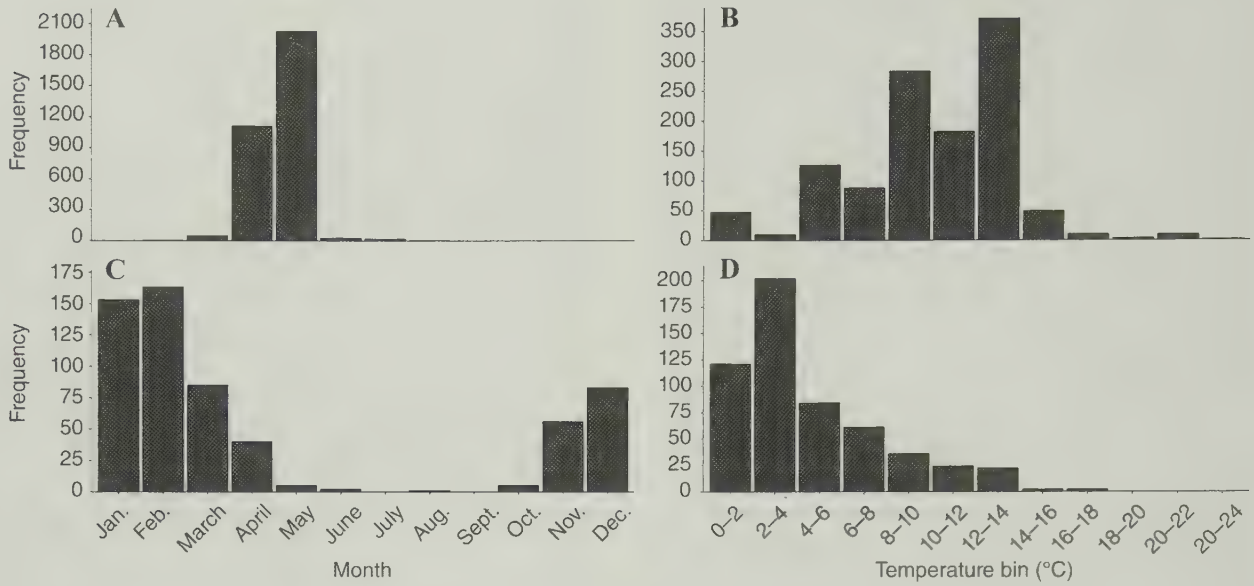

Figure 3

Frequency distributions of the months during and bottom water temperatures at which (**A** and **B**) young-of-the-year (YOY) Atlantic cod (*Gadus morhua*) and (**C** and **D**) those age 1 or older (age 1+) were captured in Rhode Island. The YOY Atlantic cod were sampled during a monthly trawl survey conducted by the Rhode Island Department of Environmental Management in 1979–2018, and age-1+ Atlantic cod were sampled during the trawl surveys conducted by the Graduate School of Oceanography, University of Rhode Island, in 1959–2018.

primarily utilizes Narragansett Bay and the Rhode Island coastal zone during the spring when water temperatures are colder.

In the URIGSO and RIDEM (Fig. 1D) trawl surveys, age-1+ (juvenile and adult life stages combined) individuals were caught primarily in waters of Rhode Island and Block Island Sound, but observations of juveniles and adults at the mouth of Narragansett Bay were frequent in the URIGSO trawl survey prior to 1975. In the URIGSO trawl survey, Atlantic cod (n=589) were almost exclusively captured between October and June (99.8%) and at the mouth of Narragansett Bay (97.5%), corresponding to temperatures below 15.0°C (95% highest density interval: 0.9–13.6°C) (Fig. 3, C and D). In the RIDEM survey, age-1+ Atlantic cod (n=63) were captured at depths between 19.5 and 39.9 m (95% highest density interval: 19.5–38.1 m) and at bottom water temperatures between 0.0°C and 19.2°C (95% highest density interval: 4.0–15.0°C). Juvenile (n=40) and adult (n=23) Atlantic cod captured in the RIDEM survey did not appear to have different temperature or depth preferences (Wilcoxon rank-sum test: P>0.05). Although few Atlantic cod were captured in the URIGSO or RIDEM trawl surveys between June and October, landings data from MRIP document catches of Atlantic cod in Rhode Island during all sampling waves, primarily outside of state waters (Fig. 4A). These landings data, therefore, indicate continued presence of age-1+ Atlantic cod farther offshore during the summer months.

Evaluation of a recent population trend

Landings in both the MRIP and VTR data sets increased from the early to late 2000s and fluctuated near the increased level thereafter (Fig. 4), an increase that is consistent with anecdotal reports from recreational anglers in Rhode Island. However, MRIP sampling does not occur during the winter months, when effort in the recreational fishery for Atlantic cod peaks in Rhode Island, making it more difficult to detect and interpret trends. Both the URIGSO and RIDEM trawl survey data sets indicate increases in catches of age-1+ Atlantic cod during the late 2000s after a period of low catches beginning in the 1990s (Fig. 5). After 2000, levels of total catch of Atlantic cod in the RIDEM survey are similar to those observed during the 1980s, but contemporary catches in the URIGSO trawl survey were only a fraction of those recorded around 1970. However, the limited catch of age-1+ Atlantic cod in both surveys makes it difficult to draw definitive conclusions.

The only life stage consistently observed in high abundance through time was YOY Atlantic cod in the RIDEM trawl survey (Fig. 5B), in which a pronounced increase in annual CPUE began in 2002. When compared with the VTR landings data, YOY mean annual CPUE in the RIDEM trawl survey was significantly correlated at a lag of 2 years both to future landings by the party and charter fleets (r=0.688, P=0.005) and to future landings by commercial vessels (r=0.586, P=0.022). Although the

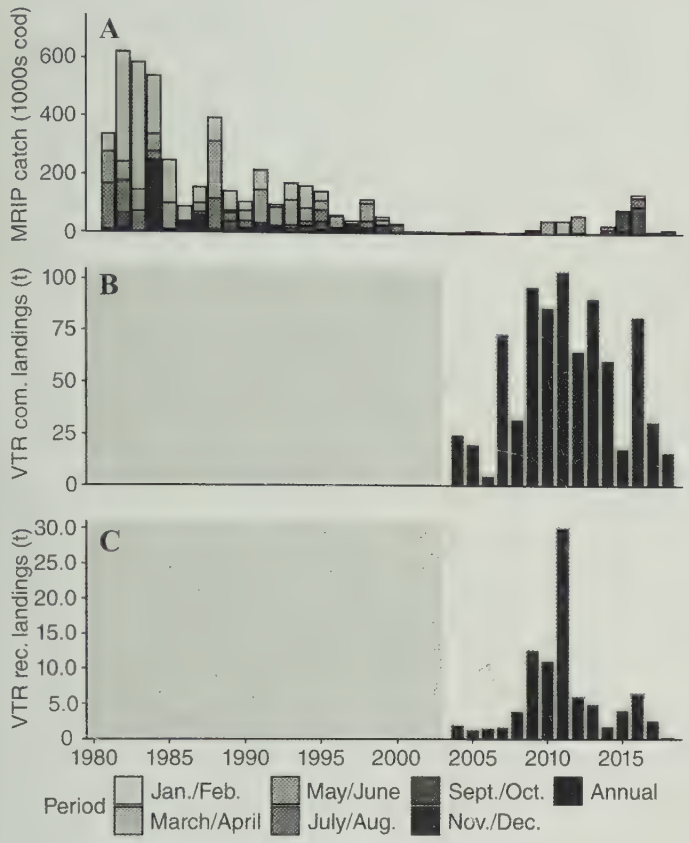

Figure 4

Abundance of Atlantic cod (*Gadus morhua*) in waters of Rhode Island from fishery-dependent sources of landings data, separated into bimonthly bins unless data were annual. Abundances shown include the following data: (**A**) landings of Atlantic cod recorded by the Marine Recreational Information Program (MRIP) during 1981–2018 and landings from the NOAA Northeast Fisheries Science Center vessel trip report (VTR) program for (**B**) commercial and (**C**) party and charter (recreational) fishing activities conducted in NOAA statistical area 539 during 2004–2018. Bimonthly bins match the sampling waves of the MRIP. Gray shaded areas indicate the periods for which no data are available.

correspondence of abundance of YOY Atlantic cod in Rhode Island state waters to overall abundance of Atlantic cod in SNE is unknown, this trend indicates that an increase in abundance of Atlantic cod has occurred in this region during the last 2 decades and has contributed to this fishery.

Investigation of links between abundance and environmental processes

Significant environmental covariates were found only for the GLM fit to CPUE of YOY Atlantic cod. No statistically significant correlations were found between abundance of YOY Atlantic cod and monthly mean wind speed, monthly mean wind direction, the North Atlantic Oscillation winter index, or monthly rain and snow accumulations. However, a strong negative relationship was identified with bottom water temperature in February (P=0.002, deviance explained=27.2%; Fig. 6). The inclusion of any other months did not provide a significant improvement in the BIC of the GLM fit, indicating that the mean bottom water temperature in February, the coldest month of the year in Narragansett Bay, is the primary tested environmental condition driving variability in abundance of YOY Atlantic cod.

Discussion

The results of this study reveal that early life stages of Atlantic cod were frequently observed in Rhode Island state waters. Larval Atlantic cod were collected throughout Narragansett Bay in 2001–2008 and 2016–2017 between the months of February and May at sizes indicating the presence of newly hatched larvae and late-stage larvae preparing for settlement or in the process of settling (Fahay et al., 1999). The observed pattern of peak abundance for larval Atlantic cod in the southern and northeastern portions of Narragansett Bay may be due to larval transport from ocean intrusion of water through the eastern portions of Narragansett Bay and the estuary's mean counter-clockwise circulation (Pfeiffer-Herbert et al., 2015). The estimated ages of the larval Atlantic cod caught in 2016 and 2017 indicate that they were spawned between mid-December and mid-February. However, there is significant uncertainty in this estimate due to 3 factors: the variability of larval growth, the use of growth curves fit with data from surveys conducted on Georges Bank (Green et al., 2004) to estimate age, and the role of temperature in larval growth and mortality rates of Atlantic cod (Buckley et al., 2004). It is noteworthy that the difference in distribution of estimated spawning dates was statistically insignificant between 2016 and 2017 despite shifts in the temporal, thermal, and size distributions of collections. The estimated spawning window matches those of previous research (Kovach et al., 2010; Loehrke, 2013; Zemeckis et al., 2014a) and the historical peak of commercial fishing activity in SNE (Serchuk and Wood[1]), all of which appear to be temporally aligned (Zemeckis et al., 2014b).

The spawning location from which Atlantic cod larvae collected in Narragansett Bay originate is unclear. Although spawning activities have been observed in the SNE region (Wise, 1958; Loehrke, 2013), results of past investigations also indicate that larval Atlantic cod spawned in the western Gulf of Maine could reach SNE prior to settlement (Huret et al., 2007; Churchill et al., 2011). Such a link has been corroborated by genetic evidence, indicating reproductive connectivity among Atlantic cod in SNE and winter spawning groups north of Cape Cod

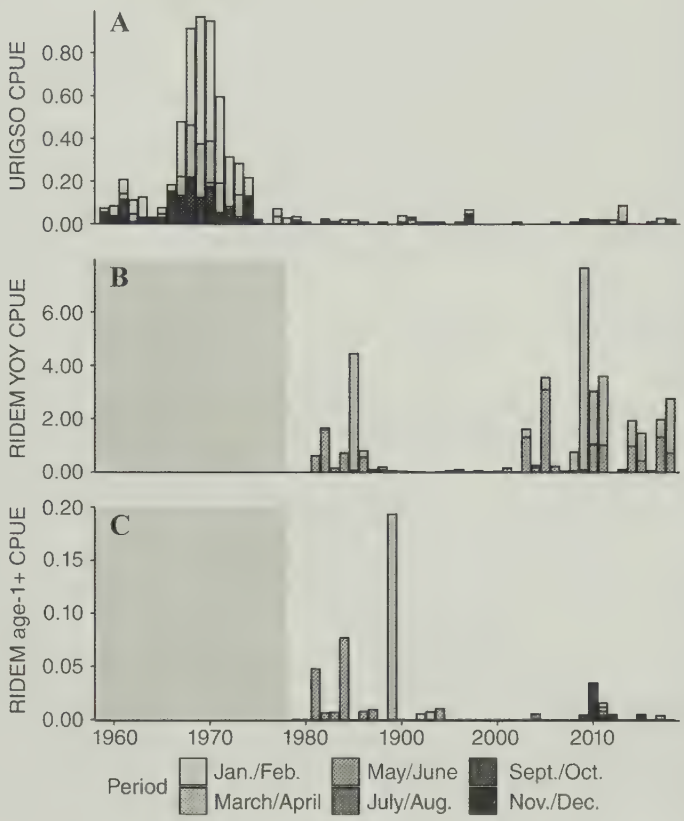

Figure 5

Abundance of Atlantic cod (*Gadus morhua*) in waters of Rhode Island from fishery-independent sources of catch-per-unit-of-effort (CPUE) data, separated into bimonthly bins. Abundances shown include the following data: (**A**) annual CPUE of Atlantic cod in the trawl survey conducted by the University of Rhode Island Graduate School of Oceanography (URIGSO) in 1959–2018, (**B**) CPUE of young-of-the-year Atlantic cod in the seasonal and monthly trawl surveys conducted by the Rhode Island Department of Environmental Management (RIDEM) in 1979–2018, and (**C**) CPUE of Atlantic cod that were age 1 or older (age 1+) in the RIDEM seasonal and monthly trawl surveys conducted in 1979–2018. Gray shaded areas indicate the periods for which no data are available.

and at the Great South Channel and Nantucket Shoals (Wirgin et al., 2007; Kovach et al., 2010). However, 42 larvae of the size at first hatch (3.3–5.7 mm TL; Fahay et al., 1999) were captured between 2016 and 2017. Although the egg stage can last up to 60 d (Fahay et al., 1999), the approximate amount of time it would take for eggs spawned in the western Gulf of Maine to reach SNE (Huret et al., 2007; Churchill et al., 2011), these observations indicate that at least some of the captured larvae came from local spawning. On the basis of studies of circulation south of Rhode Island, it is plausible that eggs and larvae spawned in the vicinity of Block Island or Cox Ledge (Fig. 1A) during winter, as documented by Loehrke (2013), would reach Narragansett Bay prior to settlement (Kincaid et al., 2003; Luo et al., 2013; Liu et al., 2016a, 2016b). The results of this work therefore provide preliminary insight into the relationship of Atlantic cod in SNE to spawning groups throughout U.S. waters and motivate further investigation to inform ongoing research into Atlantic cod stock structure (Annala[6]).

Young-of-the-year Atlantic cod were also observed throughout Rhode Island state waters. The presence of these Atlantic cod along the southern coast of Rhode Island, concurrent with observations in Narragansett Bay, indicates that larvae likely also settle in this area. In waters of Rhode Island, YOY Atlantic cod appear to have a wide temperature tolerance, a finding that is consistent with those of previous studies (Fahay et al., 1999). However, the facts that almost all of these fish were observed at bottom water temperatures <12.0°C and that fall observations occurred at a mean depth of 24.9 m indicate that YOY Atlantic cod may seek thermal refuge in deeper waters outside of Narragansett Bay as temperatures rise in the spring, and this result is consistent with research conducted in the Gulf of Maine (Grabowski et al., 2018). Although Fahay et al. (1999) noted that the rare presence of juvenile Atlantic cod inside Narragansett Bay during the 1990s made it difficult to determine their temperature and depth preferences, the reported ranges of 5–22°C and 3–34 m were close to the ranges observed for YOY Atlantic cod in this study. Young-of-the-year Atlantic cod have been found to associate with cobble substrates or areas of structural complexity after settlement (Fahay et al., 1999; Grabowski et al., 2018), but Narragansett Bay is known to be dominated by fine-grain sediments (McMaster, 1960). This sediment composition indicates that Narragansett Bay and coastal Rhode Island may be used as a settlement and early nursery habitat because of available vertical relief (e.g., macroalgae and boulders) for predator avoidance and feeding.

Although not many juvenile Atlantic cod were caught, their temperature and depth preferences, coupled with the seasonality of YOY Atlantic cod in Narragansett Bay, indicate that Atlantic cod move to deeper waters during their first summer. Given that approximately twice as many juvenile Atlantic cod as adults were observed in the RIDEM survey, these juvenile Atlantic cod may be more inclined to occupy nearshore habitats. Their depth and temperature preferences were similar, but data on recreational catches of Atlantic cod throughout the summer indicate that it is possible that adults make greater use of offshore banks in SNE, as suggested by Fahay et al. (1999) and Loehrke (2013). Specifically, recapture of Atlantic cod

[6] Annala, J. H. 2012. Report of the workshop on stock structure of Atlantic cod in the Gulf of Maine region; Portsmouth, NH, 12–14 June, 25 p. Gulf Maine Res. Inst., Portland, ME. [Available from website.]

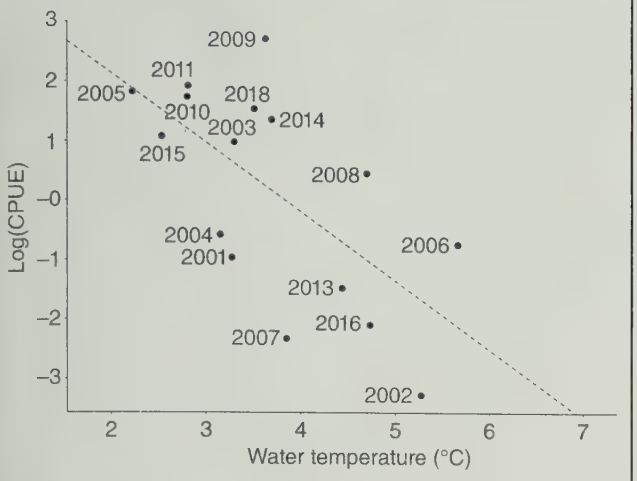

Figure 6

The approximately log-linear relationship between mean bottom water temperature in February and log-transformed mean catch per unit of effort (CPUE) of young-of-the-year (YOY) Atlantic cod (*Gadus morhua*) in March–July, during the period of observed increase in CPUE in Rhode Island state waters in 2001–2018. Water temperatures in February were recorded during trawl surveys conducted by the University of Rhode Island Graduate School of Oceanography and are used to represent values for each year, and CPUE data are from trawl surveys conducted by the Rhode Island Department of Environmental Management. The diagonal dashed line depicts a linear regression fit to the data (P<0.001, coefficient of multiple determination=0.413). Data from the surveys conducted in 2017 were omitted because of missing temperature measurements. Data from surveys conducted in 2012 were omitted because no YOY Atlantic cod were captured.

tagged in SNE by Loehrke (2013) occurred in the New York Bight, near the Nantucket Shoals and Great South Channel, and close to their point of release south of Rhode Island. Although more research is needed to develop a better understanding of offshore habitat utilization by Atlantic cod in this region, our results and those of previous studies indicate that, counter to the hypothesis of Serchuk and Wood[1], Atlantic cod may complete their life cycle in SNE. As suggested by Zemeckis et al. (2014a), we hypothesize that Atlantic cod in SNE are largely self-sustaining with some contribution of larvae from other spawning groups in the western Gulf of Maine, Great South Channel, or Nantucket Shoals.

It is difficult to assess population trends in SNE Atlantic cod with the limited data available; however, MRIP and VTR landings in nearshore federal waters support anecdotal accounts from anglers in Rhode Island of a population increase since the early 2000s. Although few juvenile and adult Atlantic cod have been caught in trawl surveys in Rhode Island state waters since the mid-1970s, catches increased slightly during the late 2000s and early 2010s. The life stage most consistently observed in these surveys was YOY Atlantic cod, for which a noteworthy increase in observed abundance began in the early 2000s. Eight of the 10 highest mean annual CPUE values in the RIDEM survey were observed between 2003 and 2018, with 6 of those occurring since 2009. However, it is unclear what proportion of settlement habitat exists within the state waters sampled as part of the RIDEM survey or how representative these areas are of regional abundance. Landings data from VTRs for NOAA statistical area 539, which encompasses Rhode Island state waters and portions of the spawning areas documented by Loehrke (2013), peaked in 2011, 2 years after the largest collection of YOY Atlantic cod observed in the RIDEM trawl survey. The identified correlation patterns, although circumstantial, do indicate that the trends in abundance of coastal YOY Atlantic cod may manifest in abundance of adults offshore.

If abundance of Atlantic cod in SNE has increased, it runs counter to expected declines in productivity of Atlantic cod as waters warm as a result of climate change. Drinkwater (2005) suggested that Atlantic cod would be outcompeted by warm-water species at mean annual water temperatures above 12°C and that the stock on Georges Bank could be expected to decline in abundance with continued warming. Although it was not possible in our study to determine the mean temperature of the habitats occupied by Atlantic cod throughout the year, data from the NEFSC fall bottom-trawl survey (available from website) indicate that late-September bottom water temperatures averaged across the approximate area in which Atlantic cod were tagged and recaptured by Loehrke (2013) (40°30′–41°15′N, 70°30′–72°0′W) can reach 16°C and have increased by ~2°C since 2000. Additionally, the temperatures at which Atlantic cod have been captured in surveys of Rhode Island state waters provide no evidence of tolerance of temperatures higher than those that have been reported in other regions. It appears, therefore, that Atlantic cod in SNE may be exposed to temperatures outside of their preferred range (Righton et al., 2010) during the summer months and have been confronted with a rapid increase in temperature in late summer during the last 2 decades. It remains possible that Atlantic cod are able to seek thermal refuge in features like the cold pool off the mid-Atlantic states during this period (Chen et al., 2018); however, these results indicate that their thermal habitat is already limited during portions of the summer and may only become more limited in the future (Drinkwater, 2005; Kleisner et al., 2017; Selden et al., 2018).

Furthermore, regression analysis of trends in CPUE of YOY Atlantic cod in Rhode Island state waters since 2000 revealed a strong negative relationship with February bottom water temperature recorded at the mouth of Narragansett Bay. This relationship agrees with work by Drinkwater (2005) and Fogarty et al. (2008), who suggested that productivity and recruitment of southern stocks of Atlantic cod would decline with increasing temperature. Yet, it is unclear if the link to winter water temperature reflects relative abundance of YOY Atlantic cod in state waters only or absolute abundance throughout the region.

Data from the URIGSO trawl survey indicate that February is the coldest month of the year in Narragansett Bay. It is possible that this annual minimum influences the prey distribution for larval and YOY Atlantic cod and that their distribution in turn affects their survival, as has been observed on Georges Bank (Lough et al., 2017). Additionally, the estimate of the spawning period produced in our study, coupled with observed Atlantic cod egg and larval development rates (Fahay et al., 1999; Drinkwater, 2005), indicates that most Atlantic cod larvae would be in the pelagic larval stage during February and that survival could be influenced by water temperature or mixing of the water column. If water temperature in February does indeed have a strong negative influence on recruitment of Atlantic cod in SNE, it raises yet more questions about how the regional population has increased in abundance. Six of the 10 warmest Februarys observed in the URIGSO trawl survey have occurred since 2002, the period of apparent increase in abundance of Atlantic cod. Because wind direction and speed were found to have no significant relationship with abundance of YOY Atlantic cod, and given the finding of Hare et al. (2015) that wind dynamics may play less of a role in successful settlement of Atlantic cod than previously thought, the abundance patterns observed in our study appear not to be due to differences in transport. However, a more thorough study is needed to conclusively rule out such dynamics in SNE.

A recent increase in abundance of Atlantic cod in SNE would also be anomalous relative to other documented changes in the regional ecosystem. Atlantic cod were most abundant in the URIGSO trawl survey prior to 1975, when data from the NEFSC spring and fall bottom-trawl surveys indicate water temperatures across the continental shelf of the northeastern United States were ≥2°C colder than they have been in recent years. As waters warmed, abundance of Atlantic cod and other cold-water species declined sharply in Narragansett Bay as the ecosystem underwent a significant regime shift during the 1980s (Collie et al., 2008) toward a warm-water, pelagic-dominated community that also has been detected in the rest of Rhode Island state waters by the RIDEM trawl survey. Given the increase of bottom water temperature and abundance of warm-water species in the last 2 decades, it is unclear what conditions have allowed an increase in abundance of Atlantic cod in the region, what time scale at which warming has affected their productivity, or how their role in the ecosystem has evolved. However, their apparent temperature preferences and the negative influence of winter temperatures on YOY abundance indicate that regional abundance will likely decline in the future.

The results of this analysis indicate that Atlantic cod in SNE may complete their life cycle within SNE waters and that the population is likely to be at least partially self-sustaining. Atlantic cod in this region appear to have increased in abundance despite evidence of limitations to available thermal habitat and recruitment due to climate change. However, several knowledge gaps remain that will be critical to effective management of Atlantic cod in SNE. First, additional work needs to evaluate the reproductive connectivity among Atlantic cod in SNE and other regions, including the New Jersey coast, as a part of ongoing investigations into Atlantic cod stock structure (Annala[6]), and to determine the degree to which the increased abundance described here is due to local spawning and to contributions from other spawning groups. Tagging efforts will also allow greater characterization of habitat utilization by juvenile and adult Atlantic cod in the region. Expanded survey efforts and a complete understanding of regional settlement, sources of early-life-stage mortality, feeding, and spawning habitats will aid in both monitoring abundance and assessing the vulnerability of this population to continued warming. Understanding how this southernmost group of indigenous Atlantic cod is interacting with temperatures at the upper end of their tolerance will be key both to successfully managing this species in SNE and to developing a better picture of how Atlantic cod will respond to future climate change throughout their global range.

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Revisiting the life history of yellowtail jack (*Seriola dorsalis*) in the Southern California Bight: new evidence for ontogenetic habitat shifts and regional differences in a changing environment

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Abstract—Yellowtail jack (*Seriola dorsalis*) are highly prized game fish within the Southern California Bight (SCB). Despite the popularity of this species, life history and demographic information for it is scant, with one previous biological examination and no population assessments. For the study described here, we used modern analytical techniques, updating historical analyses, applied stable isotope analysis to investigate ontogenetic habitat shifts, and established a novel relationship of opercular length to fork length. We sampled 256 yellowtail jack across the SCB and Baja California, Mexico, during 2014–2016. Sizes ranged from 22.7 to 162.7 cm fork length with estimated ages of 1–22 years. Body size affected diet, with larger fish consuming a greater diversity of prey. Across all samples, we recorded 19 prey species; the pelagic red crab (*Pleuroncodes planipes*), found in 23% of stomachs, was most prevalent. Coastal pelagic fish species, detected in 62% of stomachs, made up the most common group. Larger yellowtail jack were more $\delta^{15}N$ enriched, indicating increasing trophic position, and $\delta^{13}C$ levels signify an inshore–offshore habitat transition after maturity. Our results define yellowtail jack from the SCB and Baja California as one contiguous population with consistent ontogenetic variation in diet, trophic position, and growth rate. However, fish from remote areas were older and larger, perhaps indicating de facto fishing refuges.

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Across their global distribution, carangid fish species are highly prized as both game and food fish. Prominent among this group are the several species in the genus *Seriola*, whose members are known commonly as *yellowtail*, *amberjack*, *rock salmon*, or *sailor's choice*. These species are large, highly mobile, and predatory, in most subtropical and temperate boundary current ecosystems (Vergani et al., 2008; Miller et al., 2011). Along the western coast of North America, the yellowtail jack (*S. dorsalis*) (formerly *S. lalandi*; see Martinez-Takeshita et al., 2015) ranges from Cabo San Lucas in Baja California Sur, Mexico, north to Point Conception, California (Baxter, 1960). Within U.S. territorial waters, yellowtail jack are most abundant in the U.S. portion of the Southern California Bight (SCB), a term used to denote the coastline stretching from Point Conception south to Cabo Colonet in Baja California, Mexico.

Total yearly recreational catch of yellowtail jack in California is often at least one order of magnitude greater than the entire commercial take for the same year (National Marine Fisheries Service, annual commercial landings statistics, release 3.0.4.0, available from website, accessed March 2019; Recreational Fisheries Information Network, total mortality by state, available from website, accessed March 2019). This discrepancy is evident in angler enthusiasm as well, as indicated by significant increases in the number of anglers venturing out to target yellowtail jack immediately after increased recreational catches are reported (Dotson and Charter, 2003). This increase in angling pressure also has residual effects on other, co-occurring species (Sutton and Ditton, 2005).

Although yellowtail jack captivate the angling public, aside from a small study sampling fewer than 50 individuals for stable isotope analysis (Madigan

et al., 2018), there has been no research on their life history, movement patterns, or population structure along the California coast since the mid-1950s (Baxter, 1960). Improving our understanding of the biology of yellowtail jack along the western coasts of the United States and Mexico is a critical foundation for managing this taxon for fisheries value (both for sport and as food), ecosystem benefits, and potential in aquaculture (Sicuro and Luzzana, 2016).

Responding to the prominence of yellowtail jack in landings of nearshore fisheries in southern California and Baja California after World War II, the California Department of Fish and Game (now the Department of Fish and Wildlife) completed a detailed study on the biology and demography of yellowtail jack, as well as on their movements along the California and Mexico coastlines (Baxter, 1960). This work was a comprehensive description of the fish population during 1952–1957, with large sample sizes linked to the output of the prodigious fisheries yield at the time. However, the work lacked spatial resolution, for example, with no designation among fish caught in offshore versus inshore habitats. Furthermore, practically all fish were sampled or tagged along central Baja California, as opposed to within the SCB. Although central Baja California is the center of abundance for yellowtail jack and oceanographically similar to southern California (Jackson, 1986; Bograd and Lynn, 2003), the human population of southern California has been, and remains, higher than that of Baja California, with distinct anthropogenic pressures, including relatively higher recreational fishing pressure and nearshore eutrophication from urban and agricultural runoff (Schiff et al., 2000).

Yellowtail jack are believed to migrate seasonally into the SCB, moving northward as the water warms during the summer (rarely traveling north of Point Conception, except in highly anomalous warm years; Pearcy, 2002) and retreating south along the Baja California coastline during the winter and spring (Baxter, 1960). Along the route of their cross-border migrations, these fish encounter a diverse array of anthropogenic pressures, including the world's largest fleet of commercial passenger fishing vessels (CPFVs) operating in the SCB (Love, 2006).

The combination of increased human interactions and other anthropogenic effects with changed marine conditions within the SCB in the past 60 years necessitated a revisiting of the life history of yellowtail jack. Further, despite technical advances in fisheries research methods, Baxter's (1960) findings for age, growth, and diet are still used by fisheries managers in the United States today. Investigating the life history and biology of yellowtail jack with modern analytical techniques in the area in which they are most-heavily targeted will ensure that robust data exist with which to investigate potential changes in the biology of this species. Understanding how such changes might affect both the species and the fishery requires up-to-date life history data and is necessary for proactive management of this highly sought-after species. The results of the work presented here, which examined potential ontogenetic shifts in growth rate and diet, update our understanding of the biology of yellowtail jack in the SCB and establish a baseline for more targeted investigation into the biology and ecology of the yellowtail jack at the current northern extent of its range.

Materials and methods

Study species

This study focuses on the coastal population of yellowtail jack in the northeastern Pacific Ocean. This species was originally named *S. dorsalis* by Theodore Gill in 1863, then grouped together with *S. lalandi* in 1990 by Smith-Vaniz et al. (Smith-Vaniz, 1986; Smith-Vaniz et al., 1990). There is currently some disagreement as to the name of species of yellowtail jack in the eastern Pacific Ocean, with contradictory molecular findings from Premachandra et al. (2017) and Martinez-Takeshita et al. (2015). Although we acknowledge the controversy, we proceed here as per recommendations in Martinez-Takeshita et al. (2015) and use *S. dorsalis* as the scientific name for this species.

Sample collection

A total of 271 yellowtail jack, ranging in fork length (FL) from 22.7 to 162.7 cm (mean: 79.8 cm; Suppl. Table [online only]), were collected aboard CPFVs and private fishing vessels by hook and line between July 2014 and September 2016, a period of time that encompassed an anomalous warmwater event and a strong El Niño–Southern Oscillation (ENSO) (NOAA Climate Prediction Center, Oceanic Niño Index cold and warm episodes by season, available from website, accessed January 2019). We conducted sampling at 10 locations within the SCB and along the Baja California coastline in an attempt to collect samples from as much of the range of the yellowtail jack as possible. We grouped those locations into 3 regions: inshore, offshore, and island (Fig. 1). It is important to note that yellowtail jack routinely move between these assigned regions.

Straight FL and opercular length (OL) were recorded and used to calculate an OL-to-FL scaling relationship (number of samples [n]=151). This relationship enabled estimation of FL for samples taken from heads or partial frames of yellowtail jack obtained after processing aboard CPFV or as donations by anglers. These samples were often easier to obtain and reduced the amount of fish sacrificed only for sampling purposes. In addition to measurements, sagital otoliths were extracted for age estimation, a plug of white muscle was taken from along the supraorbital crest of the head of the fish for stable isotope analysis, and the stomach was excised and immediately frozen for analysis of gut contents. Because of varying collection logistics, not all types of biological samples were successfully extracted from each fish.

Age estimation

Transverse sections of sagittal otoliths were used to estimate the age of yellowtail jack (Kimura et al., 1979;

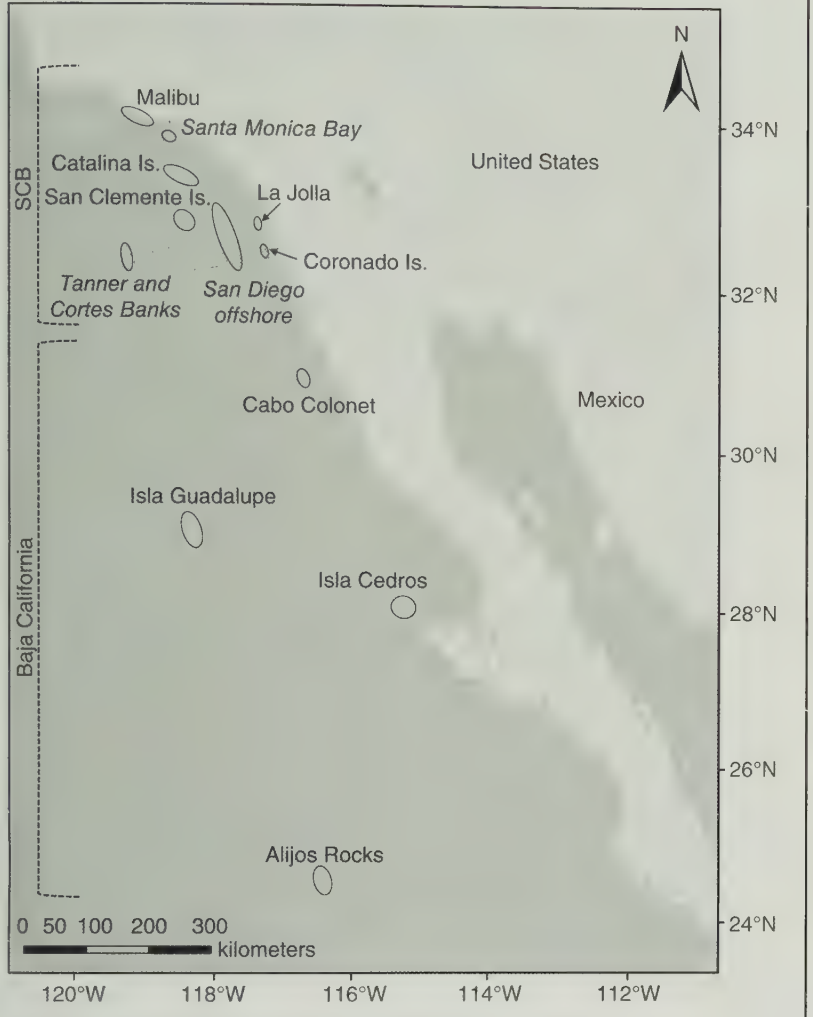

Figure 1

Map showing areas where sampling of yellowtail jack (*Seriola dorsalis*) occurred along the coastlines of southern California and Baja California, Mexico. Fish were collected aboard commercial passenger and private fishing vessels by hook and line between July 2014 and September 2016.

Choat and Axe, 1996). For the samples of yellowtail jack that were examined, both sagittal otoliths were extracted through one vertical cut at the preoperculum. The sagittae were then rinsed in deionized water and air-dried. One sagitta was weighed and measured vertically (from rostrum to post-rostrum) and horizontally (left to right across nucleus). After the position of the otolith nucleus was determined, the sagitta was mounted on a microscope slide with the nucleus falling just below the edge, leaving the rostrum exposed at a 90° angle. The sagitta was then secured by using a clear thermoplastic cement (821-3 Crystalbond 509[1], Ted Pella Inc., Redding, CA). The exposed section of the otolith was subsequently ground to the edge of the slide by using a decreasing series of wet polishing paper (400 grit [30–9 μm]) affixed to a grinding wheel (model 900, South Bay Technology Inc., San Clemente, CA). The ground sagitta was then inverted, centered, ground, and polished until reaching the nucleus at approximately 500 μm in thickness. The resulting transverse section was covered with a thin layer of Crystalbond to improve optical clarity (Zgliczynski, 2015). Polished otoliths (Suppl. Fig. 1) (online only) were examined by using a dissecting microscope outfitted with a digital camera and analyzed with digital imaging software (CaptaVision, vers. 5.1, ACCU-SCOPE Inc., Commack, NY).

After imaging, 3 separate readers examined each sample by using a single-blind method. Information concerning catch location and OL were kept from the readers during the age estimation process. Approximate ages were extrapolated by using the 1+ method to number opaque rings beginning at the annulus for each specimen (Francis et al., 2014). When the reader counts for a specimen deviated by greater than 3 years, otoliths were reexamined and new estimates made. If between-reader agreement could not be reached after reexamination, the otolith in question was excluded from analysis. Additionally, an index of average percent error (APE) (Beamish and Fournier, 1981) and mean coefficient of variation (CV) (Chang, 1982) were calculated to estimate the relative precision of age estimates between readers.

Size-at-age analysis

Size-at-age data were fit by using the von Bertalanffy growth function (VBGF) (von Bertalanffy, 1938), defined as follows:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}),$$

where L_t = the length of a fish at age t;
L_∞ = the asymptotic length or theoretical maximum length a species would reach if it lived indefinitely;
K = the growth coefficient, which is a measure of the rate that maximum size is achieved;
t = age in years; and
t_0 = the theoretical age for which length is 0 (Quinn and Deriso, 1999).

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Region-specific growth rates were generated for each sampling region and fit to size-at-age data by using the VBGF. The growth parameters K and L_∞ were also compared among regions by plotting 95% confidence ellipses around each parameter estimate (Kimura, 1980; Choat and Axe, 1996). Additionally, we calculated natural mortality (Pauly, 1980) for recently and historically sampled yellowtail jack, using VBGF parameters from Baxter (1960). Analyses were conducted by using the fishmethods (vers. 1.11-0; Nelson, 2018) and FSA (vers. 0.8.20; Ogle, 2018) packages in R (vers. 3.4.4; R Core Team, 2018).

Diet analysis

Full stomachs were dissected and weighed, with contents sorted by size through a series of graduated sieves (1 cm, 1 mm, and 0.1 mm); the empty, clean stomach was then reweighed. We sorted stomach contents from individual fish into functional groups (demersal and pelagic fish, squid, demersal crustaceans, benthic invertebrates, and amorphous material), identifying contents to species when possible (Table 1). Whole fish and invertebrates were enumerated, weighed, and identified to species. Otoliths were identified primarily by using images from Lowry (2011), vertebrae were identified by using images from Clothier (1950), and cephalopod beaks were identified by using reference samples at the NOAA Southwest Fisheries Science Center. Paired structures (otoliths, beaks, and crustacean eyes) were counted and divided by 2, to estimate the number of individual prey items. Amorphous, unidentifiable contents were quantified by subtracting the total prey weight from the difference between the full and empty stomach weights. Mean percentages were calculated for 4 major stomach content groups—fish, crustaceans, cephalopods, and amorphous material—for comparison of proportional representation across sampling location, sampling region, and body size of yellowtail jack.

Many of the yellowtail jack analyzed were collected aboard CPFV, which have fishing operations that predominantly use live bait and chum in the form of sardines or anchovies to attract gamefish to the boat. In an effort to control for the amount of CPFV chum in stomachs of yellowtail jack, we noted the number of species among the fresh, undigested chum for each sample processed. Additionally, even without active chumming, most CPFV catches come in concentrated events when the vessel

Table 1

Results from analysis of the contents of 173 stomachs from yellowtail jack (*Seriola dorsalis*) collected within the Southern California Bight (SCB) and in Baja California, Mexico, between July 2014 and September 2016. An "×" indicates that a species or taxon was found in the stomach of a fish collected in a sampling region or size group; an en dash (–) indicates that no data are available because no individual of the taxon was sampled in the region or size group. Lengths used for size groups are fork lengths calculated with an opercular-length-to-fork-length scaling relationship. n=number of samples.

		Sampling region					Size group		
Functional group	Species	Inshore	Offshore	Island	SCB	Baja	Small 0–60 cm (n=19)	Medium 60–90 cm (n=90)	Large 90–150 cm (n=37)
Fish	*Engraulis mordax*	×	×	×	×	×	×	×	×
	Sardinops sagax	×	×	×	×	×	×	×	×
	Trachurus symmetricus	×	×	×	×	×	–	×	×
	Scomber japonicus	×	×	×	×	×	×	×	×
	Sebastes spp.	×	×	×	×	×	–	×	×
	Embiotocidae	×	×	×	×	×	–	×	×
	Cololabis saira	–	×	–	–	×	–	×	×
	Halichoeres semicinctus	–	–	×	×	×	–	×	×
	Citharichthys sordidus	×	–	×	–	–	–	–	×
	Syngnathus spp.	×	–	×	–	–	–	–	×
	Synodus lucioceps	×	–	–	×	–	–	×	×
	Chromis punctipinnis	–	×	–	×	–	–	×	–
	Unidentified fish	×	×	×	×	×	×	×	×
Pelagic red crab	*Pleuroncodes planipes*	×	×	×	×	×	×	×	×
Krill	*Euphausiacea*	–	×	×	×	×	–	×	×
Rock shrimps	*Sicyonia* spp.	×	–	×	×	–	–	×	×
California market squid	*Doryteuthis (Amerigo) opalescens*	×	×	×	×	–	–	×	×
Misc. invertebrates	Isopod	×	–	–	–	–	–	×	–
	Urchin	×	–	–	–	–	–	–	×
Total number of unique species		14	11	13	13	10	4	15	16

encounters schooling, actively feeding fish. These fish are often all feeding on the same prey items. To control for the over-representation of prey items from discrete feeding events, we limited sampling to no more than 10 fish from any one CPFV trip.

To account for the multinomial (non-independent) nature of percentage data on stomach contents, we used a resampling approach to formally test the null hypothesis that the proportional diets of varying size classes of yellowtail jack do not differ. Because the diet composition of an individual fish is the result of numerous discrete choices made during foraging activities, each item consumed can be assigned to a diet category on the basis of taxonomy (or functional group) and the number of diet categories is determined by the level of dietary resolution. The total percentage of each diet category is bound between 0% and 100% and is dependent on the values of the other diet categories observed. As such, stomach content data violates several assumptions of normality and independence required for many traditional statistical approaches.

We used a tailored resampling routine following an analytical approach introduced in Barott et al. (2012) to address the multinomial nature of diet data. In this approach, mean relative diet composition for individuals from one size class is calculated as the size-class-specific centroid of the data in n-dimensional space (where n is the number of diet categories), and the mean for all individuals from across all size classes is calculated as the global centroid from all samples. For our study, the mean intercentroid distance among size classes was calculated by measuring the Euclidean distances between the centroids for each population (or size class) from the global centroid. Through resampling (10,000 iterations), we generated a null distribution of mean intercentroid distances by repeatedly scrambling size-class affiliations of diet composition data from all individuals and calculating the intercentroid distance. We then compared the actual mean intercentroid distance to this null distribution to test whether mean diets differed among size classes of yellowtail jack. If the null hypothesis (of no difference in diet composition among size classes) was rejected, the method above was repeated individually for all pairs of size classes to generate pairwise comparisons among each combination. The null hypothesis for the post-hoc test was rejected if $P<0.01$. Using Euclidean distances is, in most cases, robust across levels of aggregation of diet categories given that the approach does not de facto create higher sensitivity to an increased number of functional groups (Zgliczynski et al., 2019).

Bulk carbon and nitrogen isotopes

We analyzed samples of white muscle collected from along the supraorbital crest for both carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes to further investigate regional or size-specific trophic differences in yellowtail jack from the SCB. Although the isotopic turnover rate in white muscle of this species is currently unknown, it is assumed to be approximately 1 year (Madigan[2]). As such, their isotopic signature should reflect their aggregate diet over that time period (Peterson and Fry, 1987). Tissue samples were freeze-dried with a 2.5-L FreeZone benchtop freeze dryer (Labconco Corp., Kansas City, MO) for 48 h to remove all moisture. Samples were then pulverized by using a mechanical grinding mill (Wig-L-Bug, Dentsply Sirona, Charlotte, NC), and a 1-mg subsample (encapsulated in foil) was analyzed for $\delta^{13}C$ and $\delta^{15}N$. Analysis was performed on a Costech Elemental Combustion System ECS 4010 nitrogen and protein analyzer (Costech Analytical Technologies Inc., Valencia, CA) interfaced with a Finnigan DELTAplus XP stable isotope mass spectrometer (Thermo Fisher Scientific Inc., Waltham, MA) at Scripps Institution of Oceanography, University of California, San Diego. Isotopic values are expressed in $\delta^{13}C$ or $\delta^{15}N$, where $\delta=1000\times[(R_{sample}/R_{standard})^{-1}]$ and R_{sample} and $R_{standard}$ are ratios of the heavy to light isotope in parts per thousand. The standards used were Vienna-Pee Dee Belemnite and atmospheric N_2. The within-run run standard deviation of a glutamic standard was <0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Results

Opercular length–fork length relationship

Opercular lengths of yellowtail jack scale isometrically with FLs ($FL=4.3864(OL)^{0.9854}$, coefficient of determination [r^2]=0.951), with a strong, linear relationship between the 2 measurements. The relationship of OL to FL was plotted for 151 fish from all sampling locations (Suppl. Fig. 2) (online only). Fork lengths ranged between 28.0 and 156.0 cm (mean: 79.8 cm), and OLs ranged from 7.1 to 38.3 cm (mean: 19.0 cm). This relationship was used to estimate FL for the remaining samples collected from angler discards or partial remains of yellowtail jack. Because it is simpler to visualize overall fish size instead of OL, all subsequent length information from our study is reported in units of FL estimated with an OL-to-FL scaling relationship.

Age estimation

We estimated ages for 235 yellowtail jack from across the SCB and from 3 locations along the Baja California coast. Fish ranged from 22.7 to 162.7 cm in FL calculated with an OL-to-FL scaling relationship (Table 2). Fish had OL of 5.4–38.3 cm and ages of 1–22 years (Table 2). The APE and CV were 8.75% and 11.69%, respectively. Although there were no spatial differences in size at age and growth rate estimates at ages younger than 8, island fish reached larger sizes (>110 cm FL) and greater ages (>13 years) than both inshore and offshore fish. Additionally, fish collected in Baja California were generally larger and older than fish collected within the SCB (mean size and age: 92.4 cm FL and 9.04 years versus

[2] Madigan, D. 2016. Personal commun. Univ. Windsor, 401 Sunset Ave., Windsor, ON N9B 3P4, Canada.

Table 2

Size ranges by year class for 235 yellowtail jack (*Seriola dorsalis*) collected within the Southern California Bight and in Baja California, Mexico, during 2013–2016. Also provided are Baxter's (1960) size at age for each corresponding year class, measured and calculated by using the von Bertalanffy growth function (VBGF). In this study, it was not possible to measure the straight fork length (FL) for all sampled fish; therefore, the lengths in this table are estimates from the use of an opercular-length-to-FL scaling relationship. Mean FL and standard error of the mean (SE) are included. *n*=number of samples. An en dash (–) indicates insufficient data.

Year class		Size range (cm)		Mean FL (cm)	SE	FL (cm) from Baxter (1960)		
	n	Min. FL	Max. FL			*n*	Mean FL	VBGF FL
1	3	22.7	37.9	30.13	4.39	234	50.6	48.83
2	15	37.9	57.0	46.03	1.60	122	63.4	59.01
3	24	40.4	65.9	56.68	1.33	183	70.6	67.92
4	34	45.9	77.0	64.59	1.21	115	78.3	75.68
5	25	62.1	88.9	74.88	1.60	61	83.1	82.47
6	25	68.9	88.4	80.25	1.17	18	87.2	88.39
7	26	67.2	94.4	85.15	1.36	11	89.3	93.56
8	23	73.5	104.2	91.94	1.40	14	95.8	98.07
9	13	79.1	100.8	92.93	1.58	5	100.8	102.02
10	12	88.9	104.6	96.97	1.67	6	103.5	105.46
11	15	84.6	107.2	99.25	1.61	9	108.2	108.47
12	3	90.6	111.0	101.37	5.92	7	112.7	111.09
13	5	105.1	120.4	112.74	2.75	–	–	–
14	2	117.4	122.1	119.75	2.35	–	–	–
15	1	113.6	113.6	113.60	–	–	–	–
16	3	115.3	122.5	118.13	2.22	–	–	–
17	2	109.3	120.8	115.05	5.75	–	–	–
19	1	144.3	144.3	144.30	–	–	–	–
21	1	151.6	151.6	151.60	–	–	–	–
22	1	162.7	162.7	162.70	–	–	–	–

74.5 cm FL and 5.75 years, $P<0.005$). Natural mortality was 0.346; using Baxter's (1960) findings, we calculated a historical natural mortality of 0.261.

We observed potential differences between mean sizes of male (81.2 cm FL) and female (88.4 cm FL) fish; however, our sample sizes of sexed fish (female: n=66; male: n=44) were too low for conclusive results (P=0.087). Because we predominantly sampled angler discards, fish often were already filleted or the gonads were otherwise compromised prior to sample collection.

Stomach content analysis

Yellowtail jack within the SCB are non-discriminate mesopredators that consume a mix of pelagic and demersal fish species as well as crustaceans and the California market squid, *Doryteuthis* (*Amerigo*) *opalescens*. Of the 173 stomachs analyzed, 25.4% (44 stomachs) were empty, and the remaining 74.6% were at least partially full, with over half the contents composed of amorphous or mostly digested material (mean proportion by weight: 65.4%). Out of the remaining contents, we successfully identified 19 species. Fish species, particularly small pelagic species, including the Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), Pacific chub mackerel (*Scomber japonicus*), and jack mackerel (*Trachurus symmetricus*), accounted for 61.5% of all identified contents. The pelagic red crab (*Pleuroncodes planipes*) was the single most abundant species, present in 22.7% of all examined stomachs. Larger fish consumed a wider diversity of prey species, and the proportional representation of prey functional groups differed significantly between size classes ($P<0.01$) (Fig. 2).

Stable isotope analysis

We quantified $\delta^{13}C$ and $\delta^{15}N$ levels for 225 yellowtail jack collected throughout the SCB and coastal waters of Baja California. Values of neither $\delta^{13}C$ nor $\delta^{15}N$ varied between sampling regions or locations, but they did increase with increasing body size (r^2=0.422, $P<0.005$) (Fig. 3A). Levels of $\delta^{15}N$ increased significantly (r^2=0.596, $P<0.01$) with increasing body size, and there was no difference in the rate of increase between fish caught inshore or offshore. Values of $\delta^{13}C$ varied spatially, with $\delta^{13}C$ levels remaining relatively constant in fish caught offshore and increasing significantly with FL for fish collected inshore ($P<0.005$) (Fig. 3B).

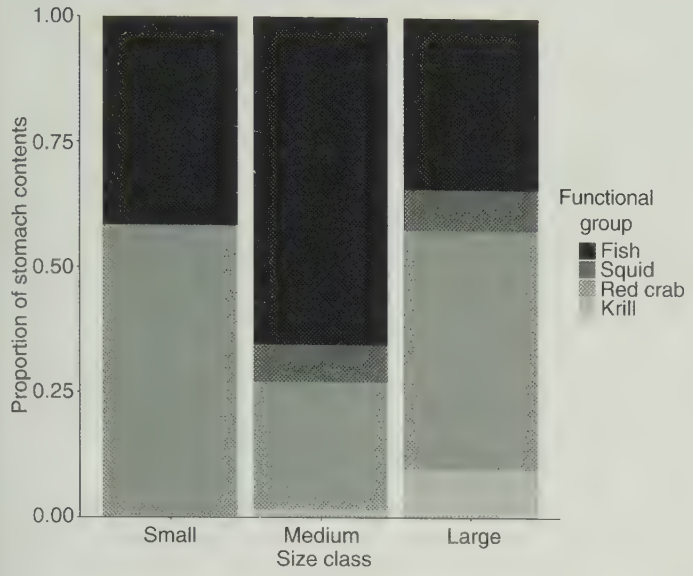

Figure 2

Proportional representation of stomach contents of yellowtail jack (*Seriola dorsalis*) collected in the Southern California Bight and Baja California, Mexico, between July 2014 and September 2016, by functional group and size class. The functional groups are krill (*Euphausiacea* spp.), the pelagic red crab (*Pleuroncodes planipes*), the California market squid (*Doryteuthis* (*Amerigo*) *opalescens*), and multiple fish species. The size classes are small (≤60 cm fork length [FL], number of samples [*n*]=19), medium (60–90 cm FL, *n*=90), and large (>90 cm FL, *n*=37).

Discussion

Our results indicate that the SCB is home to one contiguous, seasonally abundant population of yellowtail jack. Patterns observed in diet, trophic position, and growth rate are driven primarily by temporal and ontogenetic influences, and spatial variation between different regions of the SCB is less significant than originally assumed. Although these findings run contrary to anecdotal reports of geographic differences within populations of yellowtail jack in the SCB, they are supported by tagging data (senior author, unpubl. data) as well as genetic analysis (Martinez-Takeshita et al., 2015).

For this study, we examined multiple life history characteristics in order to update our current understanding of the biology of yellowtail jack within the SCB. Despite the popularity of this species as a sport and food fish, the paucity of current biological data as well as the lack of a formal stock assessment means that gauging population health or effects of current management strategies is difficult. Our goal was to update the previous demographic analysis (Baxter, 1960) with data collected from within the SCB and analyzed with modern techniques and to facilitate future research and management with a new, SCB-focused data set. We exclusively sampled fish that were caught recreationally to obtain detailed spatial information for each sample, as well as to better understand effects of recreational fishing on size classes of yellowtail jack.

Opercular length–fork length relationship

Several conversion factors for using FL to estimate total length already exist for populations of 2 species formerly considered to be a single species: yellowtail jack along the Pacific coast of North America, *S. dorsalis*, and yellowtail jack in Australia and New Zealand, *S. lalandi* (Baxter, 1960; Holdsworth et al., 2013; McKenzie et al., 2014). The creation of a robust conversion factor for expressing OL in FL means that accurate estimates of FL can be extrapolated from discarded heads of yellowtail jack. Because many anglers, fishing vessel crew members, and fish processors are happy to donate heads of yellowtail jack to researchers (senior author, personal observ.), using OL to estimate body length is an effective method of maximizing sample size and sampling efficiency given that heads also can provide otoliths for aging and white muscle, from along the supraorbital crest, for stable isotope analysis.

Age and growth estimation

This work is the first to estimate ages by using otoliths from yellowtail jack collected within the SCB. The single previous examination of yellowtail jack (Baxter, 1960) collected fish along coastal central Baja California, several hundred kilometers to the south of the SCB, and used scales to estimate ages. Sampled fish in our study were 1–22 years old and 22–156 cm FL, and the largest and oldest individuals were approximately equal in length and age to the largest fish of another species of yellowtail jack, *S. lalandi*, collected in New Zealand and Australia (Stewart et al., 2004; McKenzie et al., 2014). The similarity in size and age was surprising considering anecdotal accounts of yellowtail jack being consistently larger in waters of New Zealand than in the northeast Pacific Ocean.

We saw no differences in calculated growth rates and maximum lengths between inshore, offshore, and island habitats within the SCB. However, yellowtail jack collected from central Baja California were significantly larger and older than fish sampled from the SCB (mean size: 92.4 cm FL versus 74.5 cm FL, $P<0.005$) (Fig. 4). The differences in calculated size at age as well as in L_∞ between fish from Baja California and those from SCB were driven by the largest (>115 cm FL) fish, which were all collected from Islas Cedros and Guadalupe in Baja California. Both islands are known by anglers as prime locations to catch large yellowtail jack, with anglers at Isla Guadalupe routinely catching fish over 25 kg (Ben-Aderet, 2017). Fish over 20 kg are extremely rare within the SCB (Bellquist and Semmens, 2016), but

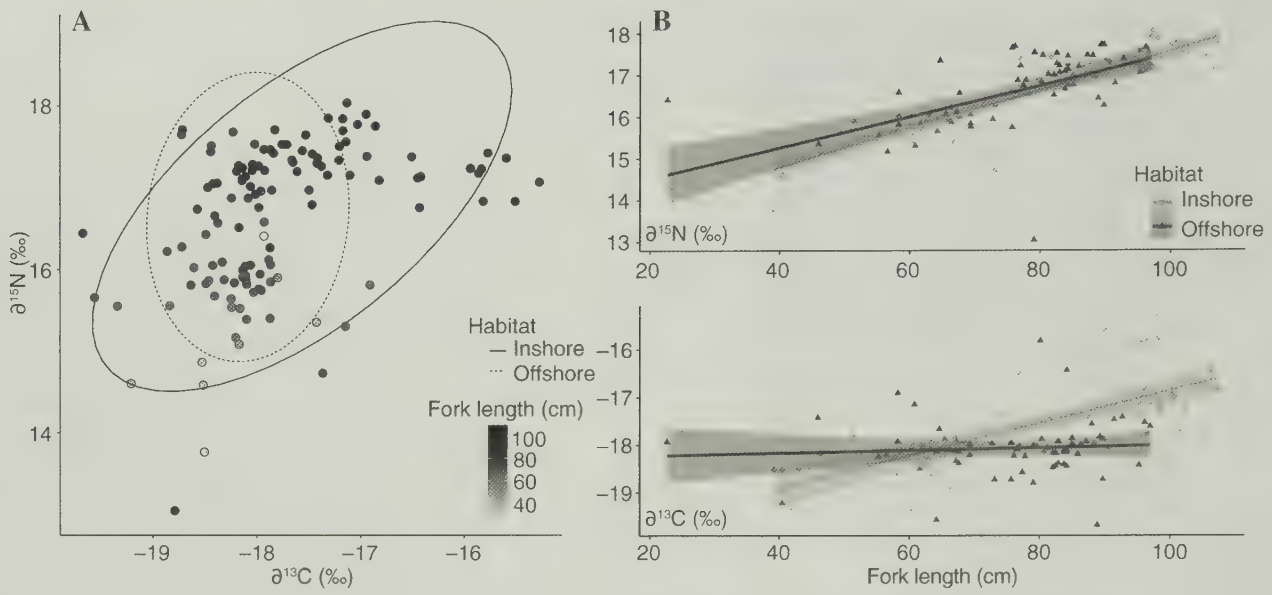

Figure 3

(**A**) Relationship of carbon ($\delta^{13}C$) to nitrogen ($\delta^{15}N$) stable isotope levels, given in parts per thousand (‰), for yellowtail jack (*Seriola dorsalis*) collected in inshore and offshore habitats in the Southern California Bight and in Baja California, Mexico, between July 2014 and September 2016. Darker shading of points indicates larger fish size, and ellipses represent 95% confidence intervals. Offshore $\delta^{13}C$ and $\delta^{15}N$ values are almost completely within those of inshore sampled fish. (**B**) Relationships of $\delta^{15}N$ (top panel) and $\delta^{13}C$ (bottom panel) levels to fork length (FL) and sampling habitat. The shaded areas represent 95% confidence intervals. The point where the lines for inshore and offshore fish intersect corresponds with the size at which yellowtail jack are thought to transition from offshore to inshore habitats.

results of genetic analysis (albeit with low sample sizes: 4 in the SCB and 10 in central Baja California) reaffirm the theory of a single contiguous population in the SCB and Baja California (Martinez-Takeshita et al., 2015). However, it is currently unknown if yellowtail jack in waters off Isla Guadalupe leave the island and venture north into the SCB or are year-round residents and, therefore, isolated from the general population in the SCB.

Sizes of fish in Baja California: evidence of a possible refuge

Working under the notion of one contiguous population, we assume that the truncated L_∞ of yellowtail jack from the SCB was primarily due to elevated fishing pressure and mortality in the SCB, although generally cooler ocean temperatures in the SCB versus Baja California and differences in forage assemblage might play a role (Stewart, 2011; Abbink et al., 2012). The relative lack of pressure at Isla Guadalupe is likely a result of isolation and distance from both mainland population centers and the nearest fishing port. Because most of the total take of yellowtail jack in the SCB is recreational rather than commercial, remote and isolated areas are more likely to serve as de facto refuges from fishing pressure (Stuart-Smith et al., 2008).

The hypothesis that remote regions of the SCB and Baja California coast serve as virtual refuges carries with it potential for unexpected climate-mediated effects (Perry et al., 2005). Because the SCB is the northern extent of the range of this species, northward range expansion could lead to increased fishing mortality due to yellowtail jack overwintering in the SCB (and, therefore, spending more time closer to elevated recreational fishing pressure). Such range effects are a real possibility because southern California's marine environment is warming and, in turn, would mean more yellowtail jack year-round in the SCB and associated increases in fishing pressure and mortality (Gillanders et al., 2001; Hobday and Evans, 2013; Champion et al., 2018).

Comparisons of size-at-age estimates

To update our understanding of the biology of yellowtail jack in the SCB and to compare our estimates of size at age with previous work, we estimated ages by using transverse-sectioned sagittal otoliths. Previously, Baxter (1960) estimated ages of yellowtail jack with annual growth rings on scales. His length-at-age estimations are the sole such work on yellowtail jack and are still used by fisheries managers. In the SCB, fish heads are readily available as angler discards; therefore, obtaining sagittal otoliths to estimate ages, although time-consuming, is relatively simple. When possible, we collected scales as well, but we were unable to replicate Baxter's (1960) methods and to obtain reliable age

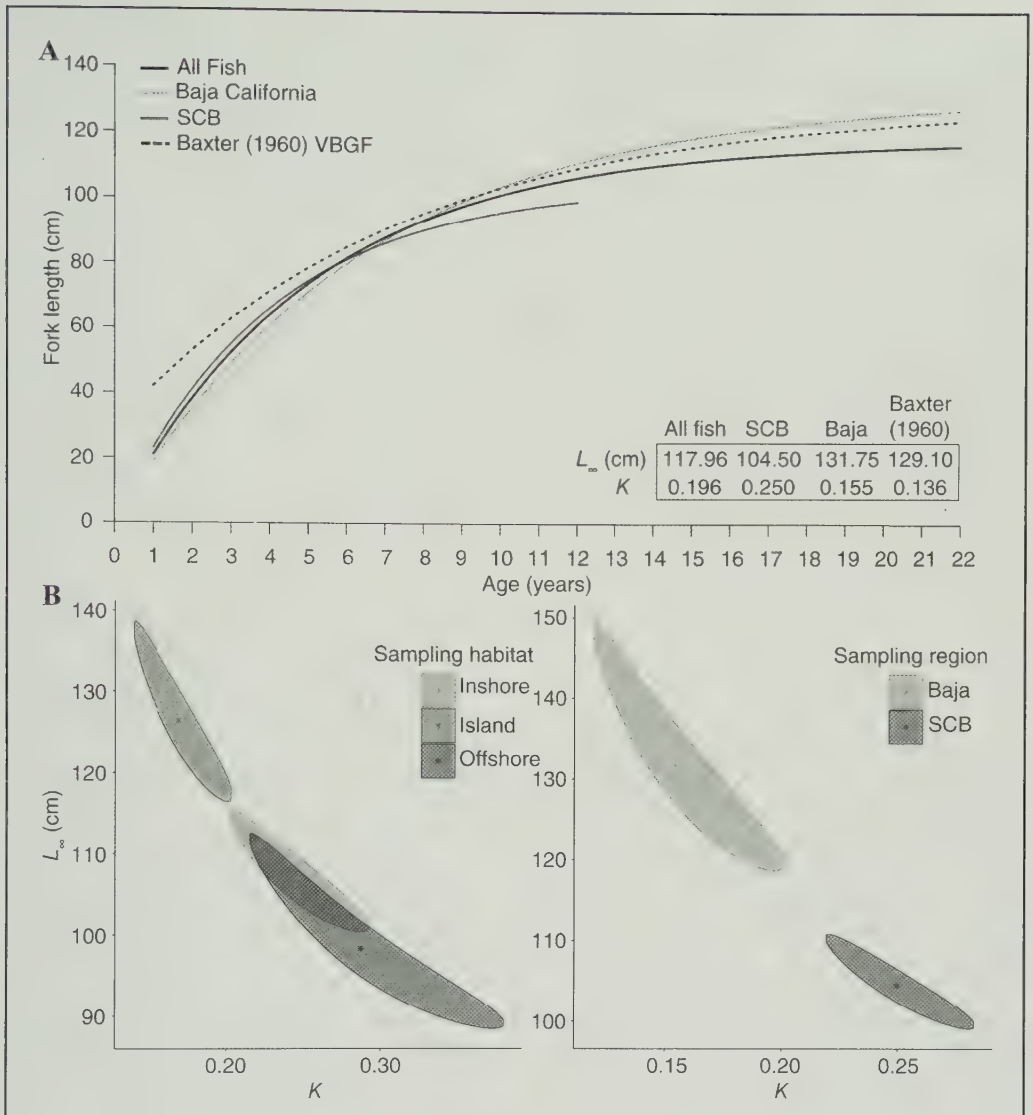

Figure 4

(**A**) Plot of von Bertalanffy growth function (VBGF) fitted to size-at-age data for yellowtail jack (*Seriola dorsalis*) collected between July 2014 and September 2016 in the Southern California Bight (SCB) (dark gray line) and in Baja California, Mexico (light gray line). Size-at-age data for all yellowtail jack (black line, coefficient of determination=0.84) and for fish by region are compared with the curve calculated by Baxter (1960) with a VBGF (dashed line). The asymptotic length (L_∞) and growth coefficient (K) are also provided for each group. (**B**) Growth coefficient and asymptotic length for yellowtail jack collected between July 2014 and September 2016 by sampling habitat (left panel) and sampling region (right panel) and plotted with 95% confidence ellipses around each parameter estimate following methods outlined in Kimura (1980).

estimations. However, Gillanders et al. (1999) compared age estimation methods by using otoliths, vertebrae, and scales from yellowtail jack collected in Australia, concluding that, aside from estimates for fish displaying only one growth zone, estimates of mean size at age from analysis of scales were similar to those from aging with otoliths (Gillanders et al., 1999). The primary issue with using scales to estimate age is a lack of definition in early years, primarily year 1 (Gillanders et al., 1999; Shiraishi et al., 2010). Despite this issue, Baxter's (1960) calculated values for VBGF parameters L_∞ and K are very close to our values for fish collected in central Baja California outside of the SCB. This comparability serves to further validate the results of Baxter (1960) because all samples were collected from central Baja California.

Interestingly, when reviewing age estimations and VBGF calculations from Baxter (1960), we noticed a 0.59-year (~7-month) offset in his estimation of t_0. When

plotted with the offset, Baxter's (1960) measured mean size at age for each year better approximates his calculated values (Fig. 4). It is unclear as to why this offset exists because no mention of it is made in that publication, despite the size being calculable from data plots. This offset could potentially be a correction for age estimates based on scales because Baxter (1960) claims that annuli on scales of yellowtail jack do not form until the second winter following hatching (when fish are 18 months old). The findings of Gillanders et al. (1999) support this claim as well, as they were unable to find 1-year-old fish when they used scales. Another potential explanation of the 7-month offset could be that he wanted to backdate fish ages to 1 January, given that spawning along the coasts of California and Mexico is thought to peak in mid-summer (with 1 July being 7 months after 1 January) (Baxter, 1960; Sumida et al., 1985). Unfortunately, these 2 potential explanations are simply conjecture. We were unable to obtain any of Baxter's (1960) original raw data or notes to explore hypotheses.

Early growth: issues for accurate age estimation

Yellowtail jack in the SCB have a similar overall population age structure to that of those from Australia, New Zealand, and Baja California (Baxter, 1960; Gillanders et al., 1999; Mckenzie et al., 2014). However, differences in length at age for young fish (ages 0–3) still need to be resolved. Baxter (1960) reports a mean FL of 50.6 cm (range: 37.1–63.3 cm) for age-1 fish and a mean FL of 63.4 cm for age-2 fish (range: 52.0–70.9 cm). These mean sizes are much larger than those for our age-1 and age-2 fish (mean size: 26.3 and 44.1 cm FL, respectively). This discrepancy could be partly due to our smaller sample size for fish <65 cm FL or to the different structures used for age estimation. Gillanders et al. (1999) found that estimates of age at scale-derived lengths are generally lower than age estimates from either otoliths or vertebrae and that scale and otolith readings diverged below age 4 (Gillanders et al., 1999).

However, the difference in sizes of year 1 and 2 fish could simply be due to differences in counting the first growth zone on whatever structure was used for age estimation. Our length estimates for yellowtail jack from the SCB were similar to estimates for those from New Zealand when aged in accordance to the 1+ hypothesis (Francis et al., 2014). If 1 year is added to Baxter's length calculations, they closely mirror our findings, especially the estimates for young fish (<4 years) (Fig. 4). The 1+ hypothesis states that the first growth zone is formed during autumn–winter of the fish's second year, an approximate age of 18 months. Because of this lag in formation of the first growth zone, Francis et al. (2014) recommended that readers of otoliths from yellowtail jack add 1 year to their age counts.

Gillanders et al. (1999) was unable to classify any scale-aged fish as year class 1, a very different finding than that of Baxter (1960). This issue of difficulty in classifying early year classes (1 and 2) in species of *Seriola* has been reported at least twice in the literature, both for greater amberjack (*S. dumerili*) from the Gulf of Mexico (Manooch and Potts, 1997) and for yellowtail jack from New Zealand (McKenzie et al., 2014). In both instances, the authors recommended further work to validate the position of the first annual growth zone on otoliths from fish of *Seriola* species.

Because of the difficulty of sampling wild yellowtail jack under ~20 cm FL, our study made no attempt to determine the annual otolith deposition zones. Gillanders et al. (1999) analyzed marginal increments on whole otoliths of fish aged as 2–4 years old and suggested that 1 zone is laid down per year in the Southern Hemisphere during winter (August–September). Stewart et al. (2004) believed that identification of the first annual zone is still problematic; our findings support this notion as well. Most recently, Francis et al. (2014) attempted to determine the location of the first growth zone in yellowtail jack from New Zealand. Although they failed to determine its location with any certainty, their results indicate that adding 1 year to the counted ages is the best current method and is how we estimated ages for this study. Further research validating the formation and position of the first growth zone should improve future age estimations for yellowtail jack in the SCB.

Elevated sea-surface temperatures: evidence of possible effects on populations

Climate-mediated recruitment pulses are possibly reflected in age–length frequency within the 235 fish sampled for this study. In the SCB, warmer-than-average conditions are coincident with El Niño summers (positive anomaly >0.5°C in the ENSO 3.4 region) (Chavez et al., 2002) and are thought to support spawning of yellowtail jack in the outer-SCB as well as to correlate with increased success in recruitment of yellowtail jack (Tian et al., 2012). Mean and median ages for all yellowtail jack were 6.0 and 6.2 years, respectively. These ages correspond with spawning during summer 2009. The climate of 2009 was a mild El Niño (positive anomaly of 0.9°C in the ENSO 3.4 region), with elevated ocean temperatures in the SCB (SIO[3]). Additionally, fish in the 90th percentile of our size distribution were larger than 96 cm FL and, according to our age estimations, greater than 10 years old. These fish most likely spawned between 2003 and 2006, again, a period of elevated sea-surface temperatures during summer in the SCB. The prevalence of fish resulting from spawning during anomalously warm-water conditions in the SCB, coupled with cyclical increases and decreases in yearly catch, further supports the idea that both spawning and recruitment are greater in the SCB during episodes of elevated sea-surface temperatures.

[3] SIO (Scripps Institution of Oceanography). 2019. Surface temperatures collected at Scripps Pier in La Jolla, CA, by Birch Aquarium at Scripps staff and volunteers. Data provided by the Shore Stations Program sponsored at SIO by the Division of Boating and Waterways, California State Parks. [Available from website, accessed February 2019.]

Size-mediated opportunistic predators

Yellowtail jack are best thought of as generalist, opportunistic predators (Baxter, 1960). Our analysis confirms this notion, although several prey species made up the majority of all contents of stomachs from fish sampled in the SCB. By functional group, coastal pelagic fish species, including Pacific sardine, northern anchovy, Pacific chub mackerel, and jack mackerel, accounted for the largest percentage of stomach contents (61.5%). However, by species, the pelagic red crab was the most prevalent single species across all stomachs sampled (22.7%), and crabs of this species were found in fish from all sampled areas in the SCB.

The primary driver of diet variation in sampled yellowtail jack was body size, with the number of both individual prey species and functional groups consumed increasing with body size. This relationship, combined with size-mediated increases in $\delta^{15}N$ enrichment and the lack of spatial variation in the proportion of consumed functional groups, indicates that the dominant trend in diet composition is ontogenetic rather than spatial. The case for such ontogenetic shifts is further supported by size-dependent differences in diet composition, with the diet of fish larger than 61 cm FL being proportionally more diverse than that of smaller fish (Fig. 2). In addition to an ontogenetic shift in diet, these results could also reflect an ontogenetic shift in habitat, given that yellowtail jack are assumed to transition from offshore (less diverse) habitats to inshore (more diverse) habitats as they age (Horn and Allen, 1978).

El Niño conditions and fishery-dependent sampling: effects on assumed spatial diet patterns

The prevalence of pelagic red crab in the diet of yellowtail jack reflects the period in which we sampled because early 2014 through late 2016 were anomalously warm in the SCB because of the confluence of strong El Niño conditions and the anomaly in the northeast Pacific Ocean called the *blob* (Bond et al., 2015). The presence of pelagic red crab in the SCB is a classic biological indicator of El Niño because they usually occur significantly farther south in more tropical waters but are advected northward during El Niño episodes (Lluch-Belda et al., 2005).

Although traditionally thought of as an offshore pelagic species, the pelagic red crab was widespread throughout the SCB for the majority of the sampling period as well as physically observed at practically every (inshore and offshore) sampling location (senior author, personal observ.). In addition to a lack of temporal variation in their presence, the ubiquitousness of pelagic red crab further confounded attempts to infer spatial patterns in the diet of yellowtail jack. Therefore, for yellowtail jack collected during 2014–2017, neither presence in stomachs nor isotopic signatures of pelagic red crab should be assumed to indicate necessarily that the fish in question was feeding in a pelagic habitat (e.g., Madigan et al., 2018), given the ubiquity of these crabs across habitat types during this time.

Levels of $\delta^{15}N$ and $\delta^{13}C$: effects on body size

We found no significant regional differences in $\delta^{15}N$ or $\delta^{13}C$ levels in samples of bulk white muscle; however, both $\delta^{15}N$ and $\delta^{13}C$ track with body size and $\delta^{15}N$ levels increase with increasing body size. The effect of size on $\delta^{15}N$ was unsurprising, given that larger fish feed on a wider variety of prey, a finding supported by stomach content analysis. Levels of $\delta^{13}C$ also increase with body size, however, only in fish collected inshore. Offshore fish showed no size-mediated variation in $\delta^{13}C$. Such size-mediated increases can indicate trophic partitioning within a population (Post, 2003). Considering that the difference in $\delta^{15}N$ values between fish that were the most and least enriched was more than 3‰ (13.00‰ versus 18.34‰ $\delta^{15}N$), and assuming a consistent prey base, large (>90 cm FL) yellowtail jack probably feed between 1 and 2 estimated trophic levels above their smallest conspecifics (Post, 2002).

Size-mediated effects: evidence of ontogenetic shift in habitats

Anglers and researchers have long assumed that yellowtail jack in the SCB shift from offshore to inshore environments as they grow, assumptions supported by work on congeners in Japan and in Australia and New Zealand (Sakakura and Tsukamoto, 1998; Kasai et al., 2000). Within the SCB, aside from recent isotopic analysis (Madigan et al., 2018), the case for such an ontogenetic shift has been based largely on anecdotal reports from commercial and recreational anglers. We observed that most of the biological variation in yellowtail jack from the SCB correlates with body size, not collection location. In addition, $\delta^{15}N$ and $\delta^{13}C$ enrichment, stomach contents, and diet diversity, all vary significantly with body size. Results of previous tagging work (Baxter, 1960; Gillanders et al., 2001; senior author, unpubl. data) indicate that broad-scale movements are size dependent as well, given that intermediate-sized fish (60–90 cm FL) were recaptured significantly farther from tagging locations than either small (0–60 cm FL) or large (>90 cm FL) yellowtail jack (10–100 km versus 100–1000 km). When viewed in concert, these factors indicate a likely shift from offshore to inshore habitat once fish are sexually mature.

Levels of $\delta^{13}C$ also point to a potential size at which habitat transition occurs because $\delta^{13}C$ values overlap for inshore and offshore yellowtail jack only at sizes of approximately 55–70 cm FL (the approximate size of sexual maturity). The divergence in $\delta^{13}C$ levels indicates a shift in consumption of prey from those exhibiting carbon signatures in line with pelagic environments to species associated with inshore kelp forests (Glaser et al., 2015; Koenigs et al., 2015). Levels of $\delta^{13}C$ enrichment that indicate an increase in trophic level also support the notion of an ontogenetic transition from offshore to inshore habitats. Offshore, pelagic habitats are generally more depleted in $\delta^{15}N$ in comparison with inshore habitats influenced by seasonal upwelling and other sources of nitrogen (Lajtha and Michener, 1994). Considering potentially lengthy isotopic turnover times in muscle tissue (MacNeil et al., 2006; Madigan et al., 2012),

and the robust swimming ability of yellowtail jack (Clark and Seymour, 2006), the lower $\delta^{15}N$ values in small (<60 cm FL) yellowtail jack from the inshore region could be a remnant from their juvenile phase in the pelagic environment. Conversely, higher $\delta^{15}N$ values in large (>90 cm FL) yellowtail jack collected offshore could indicate relatively brief offshore forays, perhaps for spawning.

Life history in the context of changing oceans

The results of our study update our understanding of the basic life history for a highly popular, yet under-studied and under-managed game fish. Our results point to yellowtail jack in the SCB as one contiguous population with consistent ontogenetic variation in diet, trophic position, and growth rate and indicate that global climate events affect yellowtail jack in the SCB. Whether by forcing northward range expansion, increasing fishing mortality, or changing available prey assemblages, the anomalously warm blob and El Niño conditions within the SCB during our sampling period influenced our results and confounded efforts to discern potential regional differences. Coincidentally, sampling for the sole previous analysis of the life history of yellowtail jack also occurred during extended positive and neutral El Niño periods. Interestingly, despite massive increases in anthropogenic effects along the coastlines of the SCB and northern Baja California since yellowtail jack were previously studied in the mid-1950s, most life history characteristics remain similar. Ultimately, the effects of increasing environmental variability and ocean warming on life history, abundance, and local and regional movement patterns of this species are not yet understood and require further investigation before being taken into account for potential management decisions.

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Development and testing of an ultra-low-opening trawl to improve utilization of quota of Atlantic cod (*Gadus morhua*) in the groundfish fishery of New England

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Abstract—A team of researchers, fishermen, and a netmaker in New England developed an ultra-low-opening trawl (ULOT) with a goal to reduce catches of overfished Atlantic cod (*Gadus morhua*) without loss of catches of other commercially important flatfish species. Use of the ULOT reduced catch rates of Atlantic cod by a mean of 48.0 kg/h (46.8%) compared with the use of a standard bottom trawl. It also reduced catch rates of American plaice (*Hippoglossoides platessoides*) by a mean of 9.5 kg/h (14.3%) but not catch rates of 3 other commercial species and 1 taxonomic group that also dominated catch. Length-based reductions in catch rates were observed, primarily for undersized American plaice (<30.5 cm in total length [TL]), mid-range yellowtail flounder (*Limanda ferruginea*) (36–38 cm TL), and large witch flounder (*Glyptocephalus cynoglossus*) (>40 cm TL). Mean ULOT headrope height was 0.73 m, and 9.1% of fuel was saved. Economic evaluation indicated that the ULOT can increase profitability and fishing time by 53.7% and 88.1%, respectively, confirming that it is a viable option for fishermen to avoid Atlantic cod while accessing quota of more abundant groundfish species.

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Avoiding the capture of Atlantic cod (*Gadus morhua*) by groundfish fishermen has become the new norm in the Gulf of Maine. This stock has declined to 4% of the target for maximum sustainable yield (NEFSC, 2015), and the commercial quota was 280 metric tons in 2017 (GARFO[1]), a reduction of over 90% since 2013. In the fishery in the adjacent Georges Bank, the stock of Atlantic cod has suffered a similar fate, and groundfish fishermen throughout New England now frequently choose fishing locations to minimize catches of Atlantic cod to the greatest extent practicable (Eayrs et al., 2017).

Atlantic cod are caught as part of a mixed species assemblage and the imperative to avoid them in New England has previously not been strong (Eayrs et al., 2017). Many groundfish fishermen use the same bottom trawl to target a mix of groundfish species that includes Atlantic cod, haddock (*Melanogrammus aeglefinus*), and yellowtail flounder (*Limanda ferruginea*) (Pol et al.[2]), often during the same tow (Rothschild et al., 2014). The vertical opening (headrope height) of these trawls is typically 1.5–3.0 m (J. Ford, personal commun.).

With quota of Atlantic cod so low, groundfish fishermen are now constrained by the risk of capturing their entire annual quota of this species in a fraction of available fishing time. The quota of Atlantic cod and other groundfish species is allocated annually to fishermen on the basis of their landing history and can be augmented by leasing or purchasing additional quota from other fishermen. However, leasing quota of Atlantic cod is problematic; quota of this species is not

[1] GARFO (Greater Atlantic Regional Fisheries Office). 2018. FY2017 commercial annual catch limits (ACL). [Available from website.]

[2] Pol, M. V., H. A. Carr, and L. R. Ribas. 2003. Groundfish trawl nets designed to reduce the catch of Atlantic cod *Gadus morhua*, 34 p. Mass. Div. Mar. Fish., Boston, MA. [Available from website.]

always available, and leasing prices are often substantially higher than landing prices (Lee, 2017). As a result, low quota of Atlantic cod often prevents fishermen from fully using their quota of other groundfish species, and often forces them to cease fishing before the end of the fishing season.

Around the world, many modifications have been tested to improve the species selectivity of bottom trawls (for review, see Isaksen and Valdermarsen, 1994; Catchpole and Revill, 2008; Graham, 2010; Winger et al., 2010). These efforts have primarily focused on encouraging the escape of fish of non-target species once they have passed into the trawl extension piece or codend. However, fish that enter these parts of the trawl are often fatigued or exhausted (Engås, 1994; Isaksen and Valdermarsen, 1994), and fish of non-target species must overcome these stressors to reach the modification and escape, increasing their risk of injury from collision with the trawl or other fish and possible post-escape mortality (for review, see Suuronen and Erickson, 2010).

Some efforts have also been made to modify the anterior section of a bottom trawl, including modification to the upper panel or square (van Marlen, 1993; Madsen et al., 2006), the groundrope (DeAlteris et al., 1997; He and Winger, 2010; Bayse et al., 2016a), the lower panel or belly (Milliken and DeAlteris, 2004; Bayse et al., 2016b), and the sweeps and bridles (Rose et al., 2010; He et al., 2015; Sistiaga et al., 2015). They also include increased headrope length and removal of twine from the upper panel of the trawl (Thomsen, 1993; Pol et al.[2]; King et al., 2004; Revill et al., 2006; Chosid et al., 2008; Krag et al., 2015; Eayrs et al., 2017). Known as a topless or cutaway trawl and defined in Federal Register (2004) as a trawl with a headrope at least 30.0% longer than the footrope, this trawl relies upon the upward escape behavior of fish of non-target species as they pass over the footrope and enter the trawl mouth.

In the groundfish fishery in New England, Eayrs et al. (2017) used a topless trawl and reported a 51.4% reduction in catch rates of Atlantic cod with no significant loss of catch of any flatfish species except American plaice (*Hippoglossoides platessoides*) that were undersized (below the minimum legal landing size of 30.5 cm in total length [TL]). The authors inferred a relationship between headrope height and layback distance (the horizontal distance between headrope and footrope at the bosom), and the position of headrope floats were key to the escape of Atlantic cod and retention of flatfish. Prior to this study, no topless trawl design had made it possible to avoid unacceptable losses of flatfish in the region (see Pol et al.[2]; Chosid et al.[3]), contributing to limited interest and uptake of this trawl by fishermen. Fishermen also cited the perceived revolutionary design of this trawl and concerns over headrope stability for their lack of uptake.

[3] Chosid, D., M. Pol, M. Szymanski, L. Ribas, and T. Moth-Poulsen. 2008. Further testing of cod-avoiding trawl net designs, 74 p. NOAA/NMFS Saltonstall-Kennedy Program completion report. Mass. Div. Mar. Fish., Boston, MA. [Available from website.]

Consideration had previously been given to designing a bottom trawl with a low vertical opening to avoid catching Atlantic cod. Early attempts with such a trawl were preliminarily tested in New England by Pol et al.[2] but did not show any difference in catches of Atlantic cod compared with catches obtained with a standard trawl. However, results of a recent examination of video collected during that study indicate that cod swimming close to the seabed had little or no subsequent rising behavior (M. Pol, personal observ.), and it was posited that the overhanging upper panel (square) and a vertical opening less than 2 m were responsible for this behavior of not rising and for low escapement of Atlantic cod. On the basis of this information, we theorized that a trawl without a square and with an *ultra*-low vertical opening, perhaps as low as 0.6 m from the seabed, might be a more successful option for passing below Atlantic cod and avoiding their entry into the trawl.

Here we describe efforts to test this theory, based on testing an ultra-low-opening trawl (ULOT). We also describe the results of a second preliminary effort to test the efficacy of a modified ULOT because the results of the second study indicate improvement in ULOT performance. This modified version is increasingly being used by groundfish fishermen.

Materials and methods

The ULOT was the product of a collaborative technical committee that comprised 4 commercial groundfish fishermen, 4 fishing gear technologists, and 1 net maker. It was also the result of systematic testing and evaluation, initially done by using trawl simulation software (DynamiT[4], vers. 2.1, IFREMER, Issy-les-Moulineaux, France) at the Fisheries and Marine Institute of Memorial University, Canada, and then by scale model (1:10 scale) testing in a flume tank at the Fisheries and Marine Institute. For a fuller description of the collaboration and development process, see Pol and Eayrs[5].

The performance of a full-scale ULOT (Fig. 1) was then compared against that of a standard bottom trawl (Fig. 2) over a 14-d period in May and June 2016 in the Gulf of Maine (Fig. 3). Both trawls had a 2-seam design and were constructed from 152.4-mm polyethylene netting with a twine diameter (ø) of 3.0 mm. The twine area of each trawl was 14.9 m^2 (excluding the codend), and the fishing circle of the ULOT and the standard trawl measured 36.6 and 32.9 m, respectively. The ULOT was designed to achieve a vertical opening of 0.6 m. The headrope of the ULOT measured 31.3 m, and the headrope of the standard trawl measured 24.5 m; the headrope-to-footrope

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5] Pol, M., and S. Eayrs. 2018. Developing an ultra-low-opening groundfish trawl to avoid cod and ensure a prosperous inshore fishing fleet, 69 p. Final report. [Available from Mass. Div. Mar. Fish., 251 Causeway St., Ste. 400, Boston, MA 02114.]

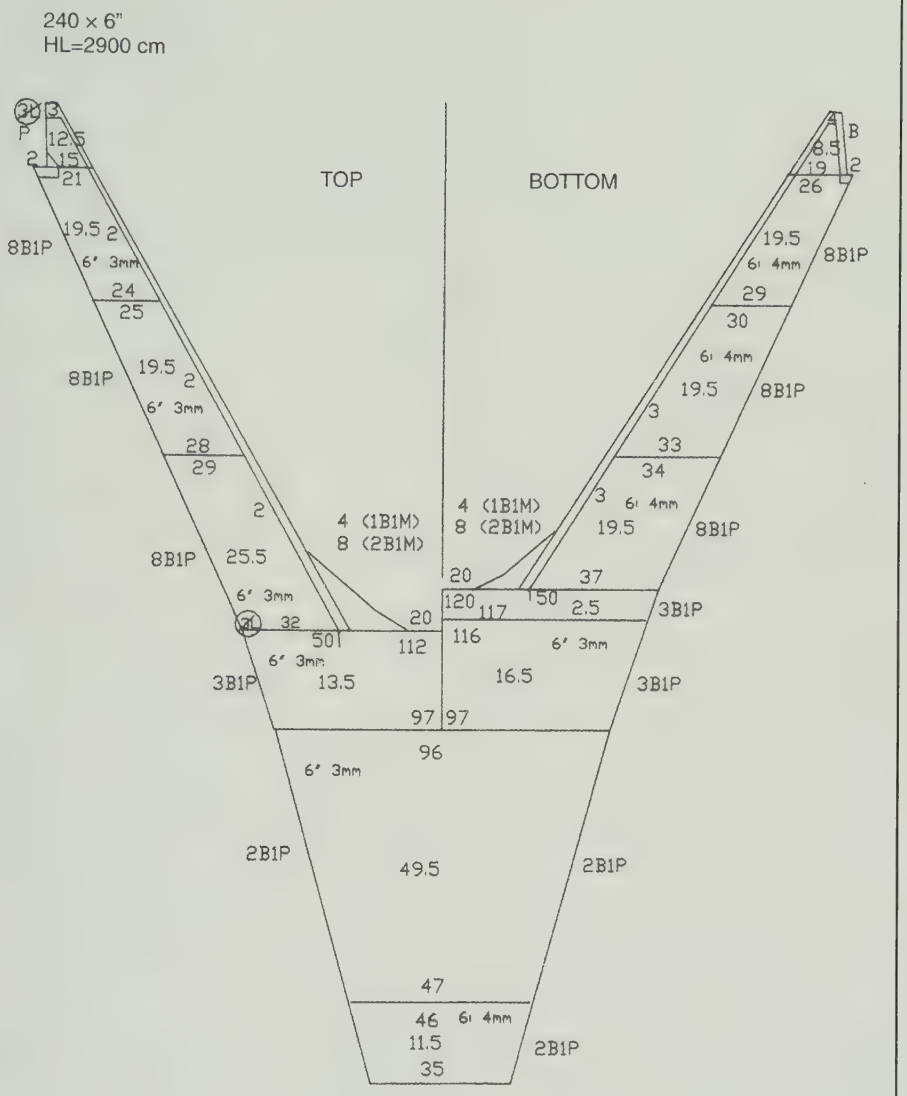

Figure 1

Technical drawing of the ultra-low-opening trawl (ULOT) used in an experiment in the Gulf of Maine over a 14-d period during May–June 2016. The ULOT was designed with a vertical opening of 0.6 m to reduce catch of overfished Atlantic cod (*Gadus morhua*) without loss of catch of other commercially important flatfish species. For each netting panel, the mesh size (in inches), twine diameter (in millimeters), panel dimensions (in number of meshes), and taper cuts are indicated. HL=headline; B=bar; P=point; and 3L=3 meshes lashed together to form a selvedge.

ratios were 1.08:1 and 0.84:1, respectively. Both trawls were fitted with an identical cookie sweep (ground line) that comprised a 12.7-mm-ø steel-wire rope threaded through 76.2-mm-ø rubber disks, and they used identical codends with 165-mm square meshes.

The headrope flotation of the ULOT comprised 8 plastic floats measuring 203 mm ø; 1 float was attached close to each wingend, and 1 float was attached adjacent to each seam joining netting panels in the wings. There was no float in the center of the headrope. The standard trawl was fitted with 16 floats measuring 203 mm ø, as per normal commercial practice for this trawl; 2 floats were in the center of the headrope, 3 floats were spread approximately 1 m apart at each wingend, and the remaining floats were spread evenly between those near the wingend and those at the center of the headrope.

Both trawls were spread horizontally by using Type 14-VFA Thyborøn semipelagic otter boards (Thyborøn Skibssmedie A/S, Thyborøn, Denmark) with a surface area of 1.75 m^2 and a total of weight of 440 kg. They were also fitted with sweeps that were 82.3 m (45 fathoms) long and constructed from 41-mm-ø steel-wire rope, including

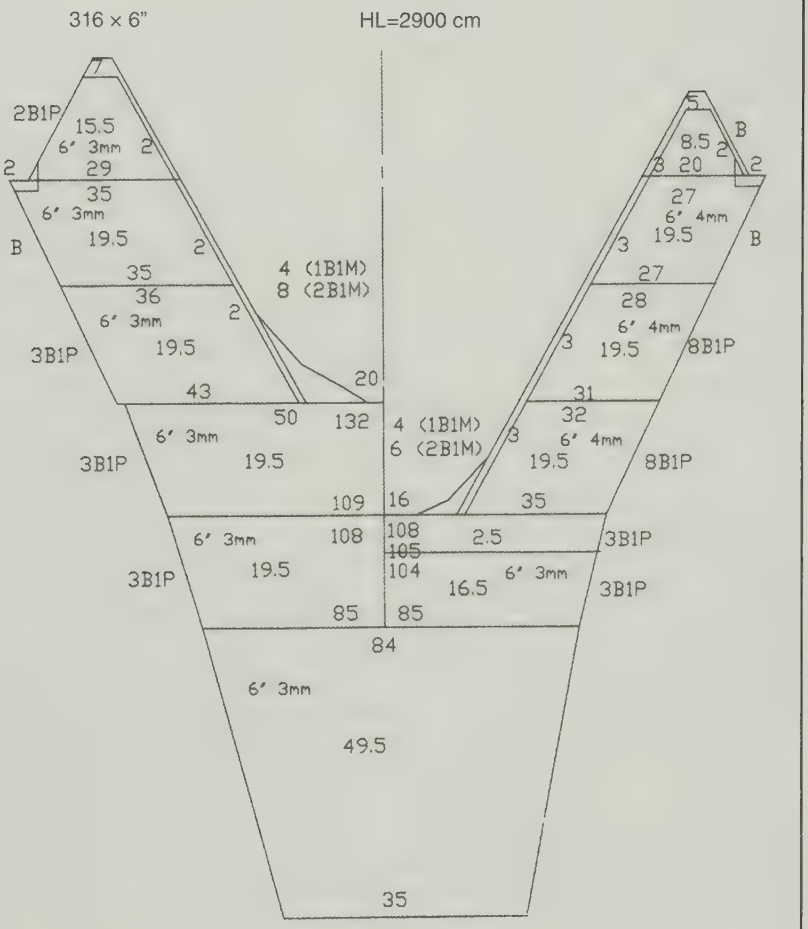

Figure 2

Technical drawing of the standard bottom trawl used in an experiment in the Gulf of Maine over a 14-d period during May–June 2016. Catches with the standard trawl and the ultra-low-opening trawl (ULOT) were compared to examine the efficacy of the ULOT at reducing catch of overfished Atlantic cod (*Gadus morhua*) without loss of catch of other commercially important flatfish species. For each netting panel, the mesh size (in inches), twine diameter (in millimeters), panel dimensions (in number of meshes), and taper cuts are indicated. HL=headline; B=bar; and P=point.

27.4-m (15-fathom) bridles (legs). On the last 2 d of field testing, the sweeps were extended by 27.4 m, and 2 floats measuring 203 mm ø were added to the center of the ULOT headrope.

Catch data from each trawl were collected from 3 pairs of hauls per day: 3 hauls of the ULOT and 3 hauls of the standard trawl in an A-B-B-A-A-B sequence. The trawl from the final haul was then the first trawl used the following day. Individual hauls in a haul pair were conducted in the same direction. The FV *Lisa Ann III*, a 16.1-m stern trawler, was used in this experiment. This vessel was equipped with a double net reel so that each trawl could be quickly deployed or stowed clear of the deck when not in use. For each haul, vessel towing speed (in meters per second), door spread (in meters), rate of fuel consumption (in liters per hour), engine revolutions (in hertz), and water depth (in meters) were recorded at 10-min intervals. The vertical opening of the ULOT was measured during 5 consecutive hauls by using pressure and depth sensors attached to the upper and lower netting panel, immediately behind the center of the headrope and footrope, respectively; these sensors were only available for 1 d. All hauls were limited to daylight hours, between 0500 and 1430.

The catch from each haul was sampled by species. All groundfish of regulated species were sorted by species into *kept* and *discarded* (undersized) categories prior to being weighed to the nearest 0.1 kg. Noncommercial species were weighed prior to being discarded overboard; discarding was not permitted during towing. All catch rates (in kilograms per hour) were standardized to a haul duration of 60 min. Total lengths of individuals of important species were measured to the nearest centimeter. Occasionally, catch of a species was excessive and necessitated collection of a subsample for lengths; the total number of individuals for each of these species at each length was then extrapolated on the basis of the proportion of the weight of the subsample to the total catch of the species.

Catch rates of regulated groundfish species and dominant species were compared graphically between trawl types and types of rigging by using equal catch plots. Paired 2-sample t-tests were applied to compare catch rates of Atlantic cod, American plaice, yellowtail flounder, witch flounder (*Glyptocephalus cynoglossus*), American lobster (*Homarus americanus*), and unclassified skates (Rajidae) for each haul. Results of a Welch's t-test were used when the results of F-tests for unequal variance indicated a significant difference ($P<0.05$). For Atlantic cod, a 1-sided t-test was appropriate given that the ULOT was designed to reduce the catch of this species, and a 2-sided hypothesis of equal mean catch rates was tested for the remaining species. All tests were performed separately on data collected before and after the modifications to the ULOT.

Length-based differences of Atlantic cod, American plaice, yellowtail flounder, and witch flounder were explored through the use of generalized linear mixed models (GLMMs). For each species, low-order polynomials were fitted to the proportions at length in the catch from the ULOT as a proportion of the total count at length from both trawls (Holst and Revill, 2009). Lengths with total counts greater than 5 individuals were used as a

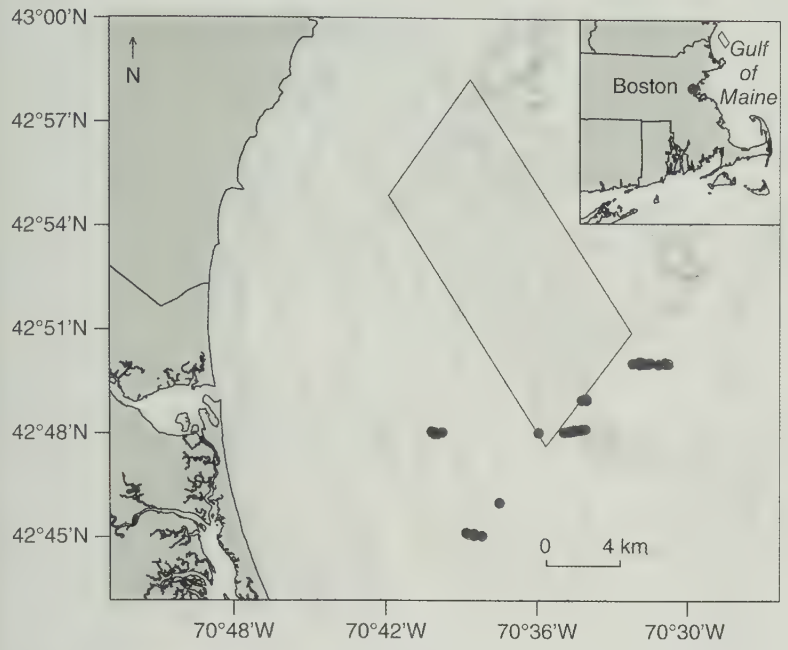

Figure 3

Map showing the start locations of individual haul pairs (black circles) conducted in the Gulf of Maine over a 14-d period during May–June 2016. For each pair, a standard bottom trawl and an ultra-low-opening trawl were hauled in the same direction. The shaded box represents the boundary of the Gulf of Maine Whaleback Cod Spawning Protection Area. Haul pairs west of the closure were conducted in a north-northeast or south-southeast direction, and haul pairs below the closure were conducted in a northeast or southwest direction. The gray lines indicate depth contours in 5-m intervals. The inset shows the sampling location relative to Boston, Massachusetts.

fixed effect, and haul was a random effect. In cases when subsampling occurred, an offset (intercept term) equal to the proportion of the subsample was used (ranging from 0 to 1) to incorporate uncertainty due to subsampling. If subsampling of lengths of both kept and discarded fish occurred for a species, the analysis was repeated, once by using the minimum of the 2 proportions and once by using the maximum, and differences (if any) were compared. A binomial distribution is appropriate to describe catches in alternating gear experiments (Wileman et al., 1996); therefore, a binomial link function was used. Following Holst and Revill (2009), we fitted a cubic polynomial model to the proportions, followed by models of decreasing complexity until all terms were significant. Model terms were assessed for differences from zero with Wald tests at $P<0.05$.

A basic economic evaluation between the 2 trawls was also completed on the basis of comparison of catch between the trawls and landings value, as determined from landing prices, fuel price, and costs of leasing quota of Atlantic cod at the time of the study. This evaluation was completed to provide greater insight into the performance of the ULOT, including its effect on fishing time and profitability.

Results

Data on the fishing and engineering performance of the ULOT (original and modified) and standard bottom trawl were collected from 67 hauls, with 31 valid haul pairs over the entire sampling period. Recorded mean towing speed was 1.4 m/s (range: 1.35–1.45 m/s), and mean fishing depth was 97.6 m (range: 54.9–116.2 m). The median interval between hauls within a haul pair was 20.0 min, and the median length of towing (warp) wire was 299.7 m (range: 182.9–337.2 m). The weather was calm throughout the experiment, and at no stage was wave height greater than 1.1 m. Mean haul duration was 1.0 h (range: 0.97–1.1 h).

The total catches in the standard trawl and ULOT were 8733.5 and 7266.8 kg, respectively, and included fish, crabs, and lobsters from 35 taxa captured over 67.0 h of trawling (Table 1). Five species and 1 taxonomic group, including Atlantic cod, American plaice, yellowtail flounder, witch flounder, American lobster, and unclassified skates, accounted for 92.0% of the total catch by weight. The mean subsampling ratio for lengths per haul and species was 0.94 (range: 0.05–1.00).

Use of the original ULOT reduced catch rates of Atlantic cod significantly by a mean of 48.0 kg/h or 46.8% (Table 2). The observed P-value was less than 0.025, indicating that the mean difference is significant whether 1- or 2-tailed tests are used. Catch rates ranged up to 224.5 kg/h, and they were lower in the ULOT in 22 of the 25 haul pairs (Fig. 4). Nearly all Atlantic cod were measured (855 individuals, extrapolated to 866 individuals; a few were discarded prior to measure). They ranged in size from 45 to 109 cm TL; lengths with total counts greater than 5 individuals ranged from 56–89 cm TL. The proportion of Atlantic cod at length in the catch from the original ULOT was best described by a linear relationship without an intercept term ($P<0.00$) (Table 3). This GLMM depicts fewer Atlantic cod at all sizes in catch from the ULOT and appeared to adequately fit the pooled data, with overdispersion (i.e., observed variance greater than modeled variance) apparent at many sizes and unclear trends apparent at the rare small (<56 cm TL) and large (>89 cm TL) sizes (Fig. 5).

The mean difference in catch rates of American plaice between the original ULOT and standard trawl was relatively small (10.5 kg/h, 14.3%) but significant (Table 2). Catch rates ranged up to 132.2 kg/h and were relatively similar in 24 haul pairs (Fig. 4), although a difference as much as 63.9 kg/h was observed between haul pairs. American plaice ranged in size from 17 to 57 cm TL, with 5725 individuals measured and an expanded count

Table 1

Composition of catch from the standard bottom trawl and the original ultra-low-opening trawl (ULOT) during May–June 2016 in the Gulf of Maine. Alternative common names for some species are given in parentheses after their recognized common names.

		Catch (kg)	
Species	Scientific name	Standard	ULOT
Atlantic cod	*Gadus morhua*	2830.1	1644.3
American plaice	*Hippoglossoides platessoides*	2385.9	2327.4
Yellowtail flounder	*Limanda ferruginea*	1640.1	1671.9
Witch flounder (grey sole)	*Glyptocephalus cynoglossus*	402.8	402.9
American lobster	*Homarus americanus*	370.2	402.9
Skates	Rajidae	357.0	285.4
Goosefish	*Lophius americanus*	275.8	201.8
Silver hake (whiting)	*Merluccius bilinearis*	110.7	59.5
Crabs	Brachyura	84.1	70.5
Sea scallop	*Placopecten magellanicus*	46.8	40.9
Haddock	*Melanogrammus aeglefinus*	61.9	25.6
Spiny dogfish	*Squalus acanthias*	31.4	50.1
Fourspot flounder	*Paralichthys oblongus*	38.7	27.7
Winter flounder (blackback)	*Pseudopleuronectes americanus*	24.6	23.9
Atlantic halibut	*Hippoglossus hippoglossus*	32.0	0.0
Lumpfish	*Cyclopterus lumpus*	11.2	15.2
Red hake (ling)	*Urophycis chuss*	6.3	4.1
Windowpane (sand dab)	*Scophthalmus aquosus*	3.8	6.4
Sculpin	Cottidae	4.6	2.3
Atlantic wolffish	*Anarhichas lupus*	4.8	1.7
Other		11.0	2.1
Total		8733.5	7266.8

Table 2

Comparison of catch rates of dominant species for the original and modified ultra-low-opening trawl (ULOT) and a standard bottom trawl in the Gulf of Maine during May–June 2016. The difference in catch rate, degrees of freedom, *t*-statistic, and *P*-value are also provided for each species.

	ULOT (original)						ULOT (modified)					
	Catch rate (kg/h)		Difference				Catch rate (kg/h)		Difference			
Species	Standard	ULOT	(%)	df	*t*	*P*-value	Standard	ULOT	(%)	df	*t*	*P*-value
Atlantic cod	102.5	54.5	46.8	23	4.52	0.000	61.8	40.3	34.8	5	2.10	0.180
American plaice	73.5	63.0	14.3	24	2.17	0.040	81.9	98.5	−20.1	5	−1.97	0.107
Yellowtail flounder	39.9	39.3	1.3	24	0.20	0.843	66.3	87.6	−32.2	5	−2.07	0.094
Witch flounder	10.3	9.5	8.3	24	1.17	0.253	16.8	21.8	−29.3	5	−2.80	0.038
American lobster	11.7	11.7	0.0	24	0.00	0.999	14.1	12.4	11.8	5	0.52	0.625
Skates	10.4	8.3	19.6	23	1.49	0.150	10.8	12.4	−15.5	5	−0.77	0.476

of 8005. Adequate lengths from data to fit a GLMM for length was judged to be 19–55 cm TL (Fig. 5). The best fit model was a second order curve, with the proportion of catch in the ULOT differing from the catch in the standard bottom trawl at small sizes (<30.5 cm TL) (Table 3). The model appeared to be a very good fit to the observed data, and there was some indication of greater reduction at the small sizes.

The catch rate for yellowtail flounder was slightly higher in the standard bottom trawl (0.6 kg/h, 1.3%) than in the ULOT but was not significantly different between trawls (Table 2). Catches in haul pairs were relatively similar for yellowtail flounder between trawls, and clusters of higher (up to 232.1 kg/h) and lower (2.5–20 kg/h) catch rates were observed. Greater variation was seen at lower catch rates (Fig. 4). Lengths of yellowtail flounder

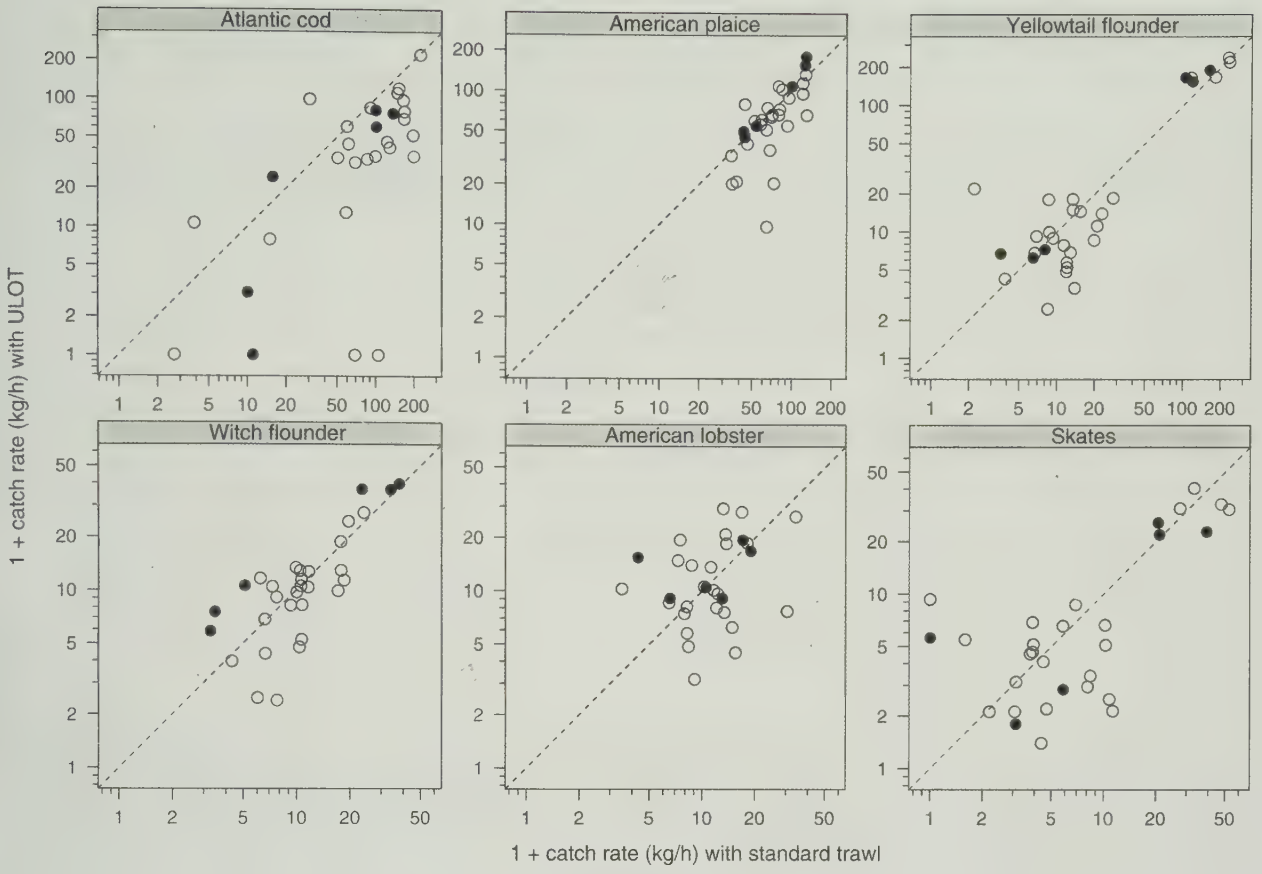

Figure 4

Plots comparing catch rates for Atlantic cod (*Gadus morhua*), American plaice (*Hippoglossoides platessoides*), yellowtail flounder (*Limanda ferruginea*), witch flounder (*Glyptocephalus cynoglossus*), American lobster (*Homarus americanus*), and skates (Rajidae) between an ultra-low-opening trawl (ULOT) and a standard bottom trawl over a 14-d period during May–June 2016 in the Gulf of Maine. All circles represent haul pairs, each of which consists of hauls of a ULOT and a standard trawl. Black circles represent haul pairs following a gear modification of the ULOT during the final 2 d of testing. The dashed diagonal line indicates the 1:1 relationship and separates haul pairs in which the catch rate was higher in the ULOT than in the standard trawl (above the line) from haul pairs in which the catch rate was lower in the ULOT than in the standard trawl (below the line).

Table 3

Mean estimates and standard errors of the mean for the parameters of the generalized linear mixed models used to analyze proportions at length of 4 dominant species in the catch from testing of the original ultra-low-opening trawl in the Gulf of Maine over a 14-d period during May–June 2016.

Species	Model	Parameter	Estimate	Standard error
Atlantic cod	Linear	β_1	−0.010	0.0022
American plaice	Quadratic	β_0	−3.605	0.6799
		β_1	0.174	0.0380
		β_2	−0.002	0.0005
Yellowtail flounder	Cubic	β_0	−61.902	19.9732
		β_1	5.633	1.8091
		β_2	−0.169	0.0542
		β_3	0.002	0.0005
Witch flounder	Linear	β_0	0.953	0.5434
		β_1	−0.028	0.0138

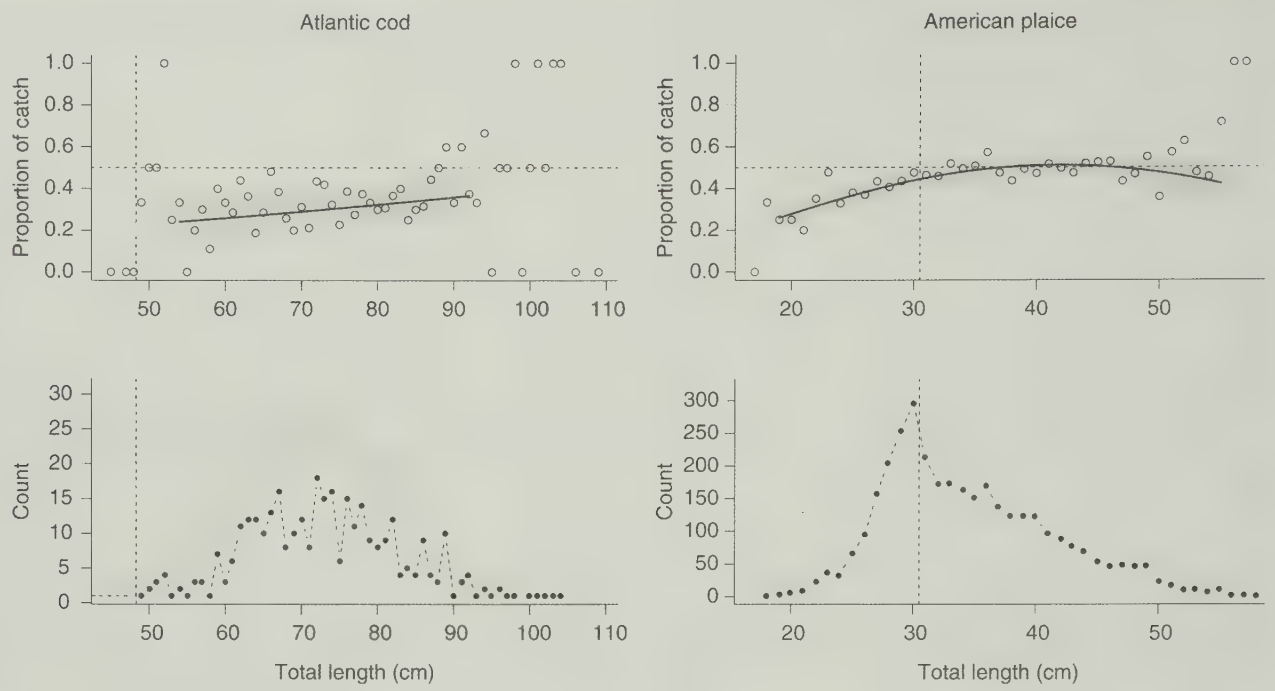

Figure 5

Proportions (top graphs) and counts (bottom graphs) at measured total lengths (TLs) of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) retained in the catch from the original ultra-low-opening trawl (ULOT) and the standard bottom trawl during May–June 2016 in the Gulf of Maine. Estimates from generalized linear mixed models (GLMMs) and observed values are included. In the top graphs, the solid black line indicates the result of the GLMM model fit with the 95% confidence interval indicated by the gray region. The circles indicate the observed count at each length of fish caught in the ULOT as a proportion of the total count at each length from both trawls. The horizontal dashed lines indicate equal proportions in the catch from both trawls (0.5). In the bottom graphs, the dots indicate counts at total lengths in catches of the original ULOT (black dots) and the standard bottom trawl (gray dots). Vertical dashed lines represent the minimum legal landing size of Atlantic cod (48.3 cm TL) and American plaice (30.5 cm TL).

(number measured: 2676; expanded count: 6069) ranged overall from 20 to 47 cm TL in 24 haul pairs, and weak data at the extremes (<24 cm TL and >44 cm TL) were excluded from analysis. The GLMM modeling resulted in a third-order polynomial as the model that best fit the data, indicating a significant loss of mid-sized (36–38 cm TL) yellowtail flounder (Table 3, Fig. 6). The observed proportions aligned closely with the selected model. Under this model, the estimated total reduction in catch of yellowtail flounder was 8.4% for fish 36–38 cm TL, or 2.6% of all legal-sized yellowtail flounder (≥30.5 cm TL).

Catch rates of witch flounder were slightly lower in the ULOT (0.8 kg/h, 8.3%) than in the standard bottom trawl and were not significantly different between trawls (Table 2, Fig. 4). Lengths ranged from 20 to 54 cm TL in 24 haul pairs (number measured: 1199; expanded count: 1239), and despite some overdispersion, a linear model provided the best fit (Table 3, Fig. 6). A small but significant loss of large (>40 cm TL) witch flounder in the catch with the ULOT was observed with a possible greater loss at the largest sizes. The estimated total reduction in catch of witch flounder was 15.8% for fish >40 cm TL, or 4.3% of all legal-sized witch flounder (≥33.0 cm TL).

Catch rates of American lobster were identical between trawls (Table 2). They were not measured for length. A mean loss of 2.1 kg/h (19.6%) was observed in the catch of skates with the ULOT but was not significantly different from the loss observed in catch with the standard trawl (Table 2). Lengths were also not collected for skates.

The mean catch rate of all 5 species and the unclassified skates with the modified ULOT (6 haul pairs) was not significantly different to the mean catch with the standard trawl, with the exception of a significant increase in the catch rate for witch flounder (Table 2). In this small sample, use of the modified ULOT reduced catches of Atlantic cod by a mean of 34.8% and increased catch rates for all 3 flatfish species by 20.1–32.2%. There was no significant difference in catches of American lobster and skates between trawls.

For every haul pair, door spread (measured in meters) was wider during the ULOT haul than during the haul of the standard trawl (Fig. 7). Overall, with the original

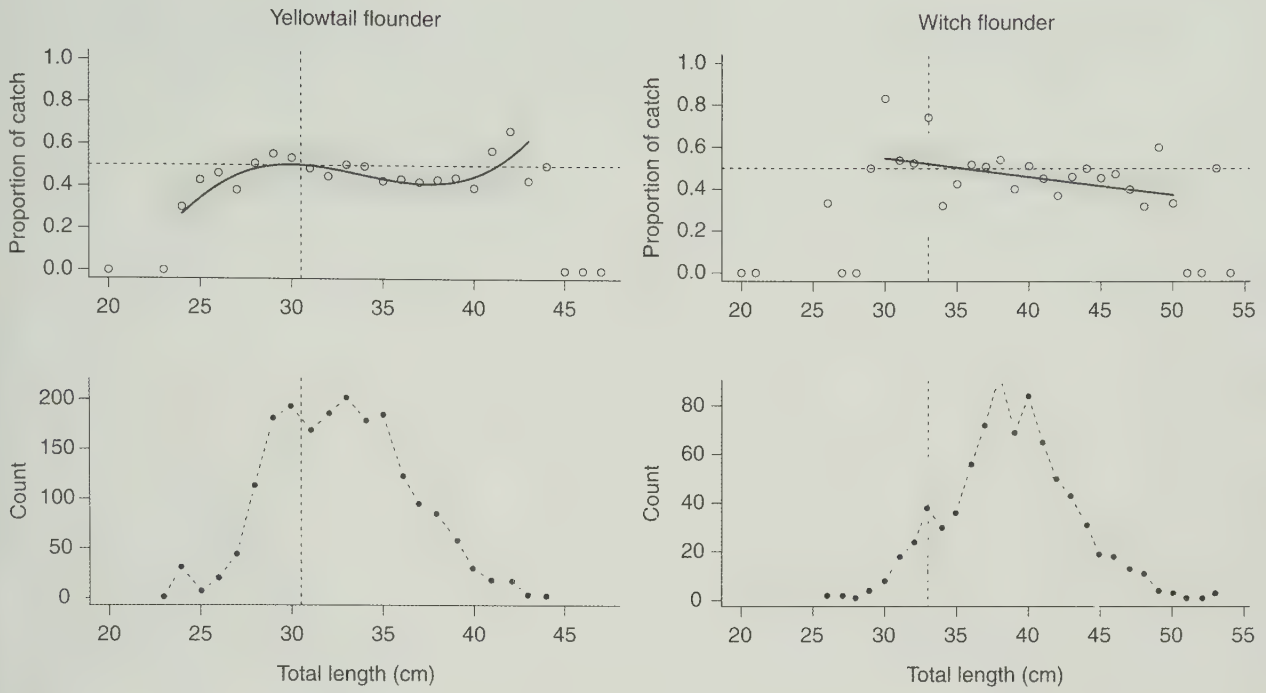

Figure 6

Proportions (top graphs) and counts (bottom graphs) at measured total lengths (TLs) of yellowtail flounder (*Limanda ferruginea*) and witch flounder (*Glyptocephalus cynoglossus*) retained in the catch from the original ultra-low-opening trawl (ULOT) and the standard bottom trawl during May–June 2016 in the Gulf of Maine. Estimates from generalized linear mixed models (GLMMs) and observed values are included. In the top graphs, the solid black line indicates the result of the GLMM model fit with the 95% confidence interval indicated by the gray region. The circles indicate the observed count at each length of fish caught in the ULOT as a proportion of the observed total count from both trawls. The horizontal dashed lines indicate equal proportions in the catch from both trawls (0.5). In the bottom graphs, the dots indicate counts at total lengths in catches of the original ULOT (black dots) and the standard bottom trawl (gray dots). Vertical dashed lines represent the minimum legal landing size of yellowtail flounder (30.5 cm TL) and witch flounder (33.0 cm TL).

ULOT, the door spread increased by a highly significant 6.5 m (10.7%) compared with the spread of the standard trawl (Table 4). Engine revolutions were lower with this trawl by 0.7 Hz (2.7%), and fuel consumption was significantly reduced by 2.4 L/h (6.5%). The mean door spread of the modified ULOT increased significantly to 17.2 m from that of the standard trawl, and there was no significant difference in engine revolutions or fuel consumption.

The mean vertical opening of the original ULOT was 0.73 m (standard deviation 0.049), and headrope height was an estimated 0.81 m when the ø of the ground rope was considered. The crew considered the original and modified ULOT to be no more difficult to use on board than the standard trawl.

A 46.8% reduction in the catch rate of Atlantic cod with the use of the original ULOT means that fishermen can increase fishing time for other species by 88.1% before exhausting their quota of Atlantic cod. This means they can conceivably utilize their quota of other groundfish species more fully and increase total landings value by 34.9% after additional fuel costs are considered (Table 5). If the entire catch of Atlantic cod is landed by using leased cod quota, and the additional fishing time is fully utilized, total landings value is increased to almost 53.7% with the ULOT.

With the modified ULOT, fishing time can increase by only 53.4% before quota of Atlantic cod is exhausted because this modification was less effective in reducing the cod catch. If the full quota of Atlantic cod is utilized, landings value will increase by 56.7% because this trawl retained a higher proportion of flatfish than the original ULOT. This percentage is increased to 73.2% if the catch of Atlantic cod is landed by using leased quota of Atlantic cod.

Discussion

The ULOT represents the first known successful attempt to reduce headrope height to avoid Atlantic cod and retain flatfish in New England. Catches of Atlantic cod were reduced by nearly 47% by using the original ULOT, and there was no significant difference in catch of yellowtail

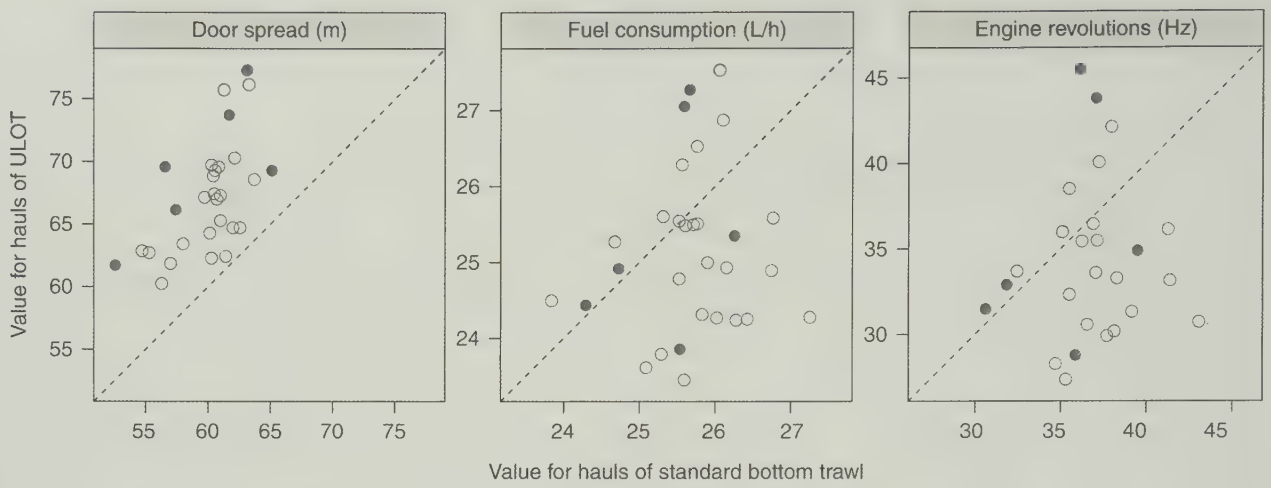

Figure 7

Plots comparing values of door spread, fuel consumption, and engine revolutions between hauls of an ultra-low-opening trawl (ULOT) and hauls of a standard bottom trawl conducted over a 14-d period during May–June 2016 in the Gulf of Maine. All circles represent haul pairs, each of which consists of hauls of a ULOT and a standard trawl. Black circles represent haul pairs following a gear modification of the ULOT during the final 2 d of testing. The dashed diagonal line indicates the 1:1 relationship and separates haul pairs in which the measured value was higher in the ULOT trawl than in the standard trawl (above the line) from haul pairs in which the measured value was lower in the ULOT than in the standard trawl (below the line).

Table 4

Engineering performance—door spread, engine revolutions, and fuel consumption—of the original and modified ultra-low-opening trawl (ULOT) compared with that of the standard bottom trawl in the Gulf of Maine during May–June 2016. The percent difference between the standard trawl and each ULOT, degrees of freedom, *t*-statistic, and *P*-value are provided for each aspect of performance.

	ULOT (original)						ULOT (modified)					
Engineering performance	Standard	ULOT	Difference (%)	df	*t*	*P*-value	Standard	ULOT	Difference (%)	df	*t*	*P*-value
Door spread (m)	60.1	66.6	−10.74	22	−9.382	0.0000	59.4	69.6	−17.15	5	−6.837	0.0005
Engine revolutions (Hz)	25.8	25.1	2.72	23	2.868	0.0029	25.3	25.5	−0.53	5	−0.254	0.4048
Fuel consumption (L/h)	37.2	33.8	9.12	20	3.385	0.0087	35.2	36.2	−2.99	5	−0.406	0.3506

flounder or witch flounder between the original ULOT and the standard bottom trawl. Losses of American plaice were significant but limited to undersized individuals. Some loss of yellowtail flounder 36–38 cm TL and witch flounder >40 cm TL was documented, but this reduction represented a small decrease of <5% of landable individuals of those species. It is possible that these individuals responded to the approaching trawl by swimming over the headrope. A loss of small American plaice (<21 cm TL) in the same fishery was also reported by Eayrs et al. (2017) during the testing of a topless trawl, and although the similar results are intriguing, they do not offer much insight into the reasons for this reduction, which remain unknown. The headline height of the original ULOT was slightly larger than desired, and a substantial reduction in fuel consumption was realized. Catches were considered typical of the commercial fishery by species, composition, and volume.

Notwithstanding a low number of haul pairs, the performance of the modified ULOT is also encouraging. Reducing the catch of Atlantic cod by almost 35% while retaining more flatfish is an improvement over the standard trawl, and we feel the efficacy of the modified ULOT should be subject to detailed evaluation in the future. This version of the ULOT has been used by several groundfish fishermen.

The original ULOT was designed to provide an effective, low-opening alternative to the multispecies groundfish trawls used in New England. Along with the topless trawl, recently evaluated by Eayrs et al. (2017) in the same

Table 5

Comparison of total catch value for 5 dominant species in the Gulf of Maine between the standard bottom trawl and the original ultra-low-opening trawl (ULOT), based on an assumed 2000-kg quota of Atlantic cod (*Gadus morhua*) and landing prices during May–June 2016. Landings of other species are prorated on the basis of hourly catch rates of kept individuals during the study (see Table 2). Fuel costs for both trawl types are based on the estimated time to land 2000 kg of Atlantic cod by using each trawl, an assumed 8 h of towing time per day, and hourly fuel consumption rate. Daily fuel consumption steaming to and from the fishing grounds was typically 190 L/d (J. Ford, personal commun.). The price of diesel fuel at the time of study was $0.63/L. Average leased cost for Atlantic cod in 2016 was $6.05/kg.

	Catch (kg)		Landing price	Catch value ($)		
Species	Standard	ULOT	($/kg)	Standard	ULOT	Difference (%)
Atlantic cod	2000.00	2000.00	8.80	17,600.00	17,600.00	0.0
American plaice	1434.15	2313.27	6.60	9465.39	15,267.58	61.3
Yellowtail flounder	778.54	1442.20	3.96	3083.02	5711.11	85.2
Witch flounder	200.98	348.62	11.00	2210.78	3834.82	73.5
American lobster	228.29	429.36	13.20	3013.43	5667.55	88.1
Total catch value				35,372.61	48,081.07	35.9
Total catch value – fuel cost				34,624.68	46,730.24	34.9
Total catch value – fuel and cod lease costs				22,524.68	34,630.24	53.7

fishery, this trawl improves utilization of quota of Atlantic cod; both trawls reduce catch rates of Atlantic cod and therefore extend fishing time before exhausting the quota of this species. In contrast to the topless trawl, which permits herding of Atlantic cod and entry into the trawl prior to escape over the headrope, the ULOT is designed primarily to pass below Atlantic cod and eliminate stress and physical injury during passage through the trawl. The ULOT also represents a less revolutionary trawl design that may be more easily adopted and accepted by fishermen. Trawls with approximately equal headrope and footrope lengths are used to pursue and capture other species in the region; therefore, the design is familiar to many fishermen. However, application of a ULOT-type design for avoidance of Atlantic cod with a very low opening was unknown prior to this work.

Use of the original ULOT provides an opportunity for fishermen to increase efficiency and profitability, compared with that achieved with the standard trawl, in the short term through reduced rate of fuel consumption. Using this trawl in the long term, fishermen can conceivably increase fishing time by 88.1% before exhausting their quota of Atlantic cod, and provided this time is available, 3 additional benefits can potentially be realized.

First, use of this trawl permits greater utilization of quota of other groundfish species. Based on data in NOAA reports for the fishing years 2011–2018 (GARFO[6]), annual landings of American plaice, witch flounder, yellowtail flounder, and winter flounder (*Pseudopleuronectes americanus*) in the Gulf of Maine have respectively averaged only 80.6%, 86.1%, 73.1%, and 27.3% of the annual catch limits for these species, and the ULOT provides an opportunity to increase these percentages. Second, use of the original ULOT reduces the need for fishermen to lease expensive quota of Atlantic cod, or to spend time searching for available cod quota, prior to the end of the fishing year. Finally, by fishing longer and more fully utilizing their quota of other groundfish species, fishermen can potentially increase total landings value by almost 54% after fuel costs are considered. Collectively, these benefits are a substantial incentive for fishermen to adopt the ULOT, notwithstanding the exclusion in this analysis of other operating costs, such as crew payments, food, and ice, which are more or less a constant proportion of operating costs irrespective of fishing time. The incentive to use this trawl is even more compelling when the variable cost and availability of leasing quota of Atlantic cod are taken into account, and the amortization period on the purchase of a ULOT is substantially less than that for a standard trawl, given that the cost to construct both trawls is similar (J. Knight, personal commun.).

It was our goal to develop a practical design that would lead to voluntary adoption of the ULOT by local fishermen. Outreach efforts are currently underway, including offering free use of 3 different sizes of the ULOT, and fishermen have already taken this opportunity and given positive feedback. This opportunity has been broadcast through a variety of means, including social media, printed announcements, and trade publications. Voluntary adoption of new fishing designs has been historically problematic (Eayrs

[6] GARFO (Greater Atlantic Regional Fisheries Office). 2012–2019. (FY2011–FY2018) commercial annual catch limits (ACL). [Available from website.]

and Pol, 2019); however, with the anticipated savings and earnings potential, we hope fishermen will readily adopt this trawl. Although not all fishermen have the capacity to increase their fishing time by 88.1% and some switch between different fisheries during the year, many fishermen are hampered in their ability to fish an entire season because of inadequate quota of Atlantic cod. Subsequently, many fishermen do have the available days to absorb some or all of this increase and realize the benefits of the ULOT. It is also worth noting that the fishermen involved in this study still use the modified ULOT.

The ULOT design is the second bottom trawl recently developed and tested in the region that has reduced catches of Atlantic cod by about half with minimal effect on catches of targeted flatfish species. These results indicate that Atlantic cod can generally be expected to swim above or rise at least 0.5 m in response to an approaching trawl, although we recognize that this behavior is inferred rather than directly observed. On the basis of the development of the ULOT and the topless trawl, we have established a baseline in avoidance of Atlantic cod through modification in the anterior end of a trawl and provided evidence that removal of the square has limited effect on flatfish catches. It remains unclear if further improvement in this part of the trawl is achievable, although greater reduction of bycatch of Atlantic cod is likely if these designs are paired with modifications to the extension piece or codend, such as square-mesh windows or codends.

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Diet of harbor porpoises (*Phocoena phocoena*) on the continental shelf off southern New England

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Abstract—Little is known about the diet of harbor porpoises (*Phocoena phocoena*) in southern New England where bycatch was a highly contentious issue since the late 1990s until recently. To fill this data gap, stomach contents were examined from 46 harbor porpoises taken as bycatch over 24 years (1994–2017) between January and May. Prey species were identified to the lowest possible taxon through hard part analysis, primarily of otoliths and squid beaks. Size and species of harbor porpoise prey overlapped little with those of gillnet catch. Average prey size was larger for adult harbor porpoises (≥140 cm total length), females, and those taken during the first half of our study (1994–2006) than for smaller porpoises, males, and those caught during the second half (2007–2017). Average total biomass consumed per stomach was 2.3 kg, an estimate that represents approximately 12–24 h of feeding. Clupeids, true hakes (*Urophycis* spp.), squids (Decapodiformes), and silver hake (*Merluccius bilinearis*) constituted 85.5% of all estimated biomass. Cusk-eels (Ophidiidae) and small flatfish species (Pleuronectiformes) were frequently consumed (found in 29.8% and 27.7% of all stomach samples), but each taxon made up less than 1% of estimated biomass because of their small size. These results could help advance ecosystem-based management by better defining the diet of harbor porpoises in the context of potential climate changes.

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Marine mammals are affected throughout their range by fisheries bycatch (Read et al., 2006; Lewison et al., 2014; Burgess et al., 2018; Gray and Kennelly, 2018) and increasingly by climate change (Learmonth et al., 2006; Simmonds and Isaac, 2007; Sydeman et al., 2015). In order to manage and mitigate these and other threats, we need to better understand the factors behind marine mammal distributions. Regular abundance surveys and associated modeling have helped discern distributions of marine mammals in some regions (e.g., Roberts et al., 2016); however, for many species, limited quantitative information exists to explain the reasons behind their distributions. Marine mammal distribution is primarily driven by prey resources for much of the year, depending on species and reproductive life history strategies. For a small marine mammal, such as the harbor porpoise (*Phocoena phocoena*), with high metabolic needs and no annual breeding migration, we expect prey distribution to be a primary factor in its distribution (Read et al., 1997).

The waters of the northwest Atlantic Ocean on the continental shelf of North America that are the primary habitat for harbor porpoises are predicted to warm at nearly 3 times the global average (Saba et al., 2016). This area has already seen documented shifts in distribution of some species (Nye et al., 2009; Kleisner et al., 2016), changes that may affect distribution and prey resources of harbor porpoises. The Gulf of Maine and Bay of Fundy stock of harbor porpoises occupies waters off the northeastern United States and its range extends from North Carolina to the Bay of Fundy and the Scotian Shelf off Nova Scotia, Canada (Waring et al., 2014). Harbor porpoises are concentrated in the Gulf of Maine and southern Bay of Fundy during the summer months and are more widely dispersed during the rest of the year, extending as far south as North Carolina from January through April (Polacheck et al., 1995; Orphanides, 2009; Waring et al., 2014). Most harbor porpoises are believed to stay in continental shelf waters throughout the year, although they have occasionally been observed along and off the shelf edge (Read and Westgate, 1997; Schofield et al., 2008; Orphanides, 2009; Waring et al., 2014).

Bycatch of harbor porpoises was one of the most contentious issues of marine mammal management in the northeastern United States for years (Orphanides and Palka, 2013). The population of harbor porpoises on the northeastern U.S. continental shelf was considered a strategic stock under the Marine Mammal Protection Act, meaning that estimated bycatch exceeded prescribed limits. As a result, gillnet time-area closures were enacted in 2013 at a time when the groundfish fishery was already under immense stress because of reduced catch allowances and a transition to catch share management (Orphanides[1]; Murphy et al.[2]). Despite these management issues and the rapidly changing ocean in which harbor porpoises live, no recent research has assessed the diet of harbor porpoises as a means to better understand distribution and potential relationships to bycatch.

For the analyses described in the last 2 published papers on the diet of harbor porpoises in the northwest Atlantic Ocean, the data used were from June through September during 1989–1994 in the Gulf of Maine (Gannon et al., 1998) and from September into December during 1985–1987 in the Bay of Fundy, Canada (Recchia and Read, 1989). No published papers have ever reported assessment of the diet of harbor porpoises in southern New England or from January to May, the area and season in which much of the bycatch of harbor porpoise now occurs (Orphanides and Palka, 2013; Hatch and Orphanides[3,4]). With this study, we aimed to fill that data gap, assessing the diet of harbor porpoises on the continental shelf of North America during the winter and early spring, examining prey relative to gillnet catch, and calculating biomass consumed. We hope that our results, by improving understanding of prey consumption by harbor porpoises, can inform ecosystem-based management as fish distributions shift (Nye et al., 2009; Kleisner et al., 2016, 2017; Saba et al., 2016).

Materials and methods

Stomach processing

Stomach samples were collected by the Northeast Fisheries Observer Program (NEFOP), part of the National Marine Fisheries Service. Fisheries observers retrieved animals incidentally caught in gillnet hauls on the continental shelf in southern New England during 1994–2017 (Figs. 1 and 2). These observers recorded numerous aspects of fishing trips and hauls, including locations and dates of fishing events, gear characteristics such as mesh size, and details on both the kept and discarded catch (NEFSC[5]). Observers brought to port for biological sampling approximately 10% of bycaught harbor porpoises from the waters of southern New England during our study period. The majority of bycatch events occurred from January through May, with 6, 7, 11, 16, and 6 stomach samples collected during each of the 5 months, respectively. Size and sex of most bycaught harbor porpoises were also recorded by observers or during a necropsy (Fig. 3).

Fifty harbor porpoises from 1994 through 2017 were collected by NEFOP in our study area and considered for analysis (Fig. 1). The stomachs of 12 harbor porpoises were retrieved from comprehensive necropsies during which life history and biological information, such as reproductive status, was gathered, and 10 other necropsies were more cursory and did not include collection of maturity information on male and female reproductive organs. The remaining stomachs did not have necropsy information available because some stomachs, particularly earlier in the time series, were extracted at sea and whole animals were not brought back to shore. Therefore, animal length was used as a proxy for maturity on the basis of studies of life history, seasonality, tooth aging, and necropsies (Read and Gaskin, 1990; Read and Hohn, 1995; Wenzel, 2000).

Of the 50 stomachs collected, 4 were either empty or contained only fragments of unidentifiable otoliths and were not included in this analysis. The remaining 46 comprised 17 females, 26 males, and 3 individuals of unknown sex. Only 1 female was known to be pregnant. Harbor porpoises that were measured for size (total length) included 10 individuals that were considered young of the year (<125 cm), 10 juveniles (125–139 cm), 23 adults (≥140 cm), and 3 individuals of unknown maturity (Fig. 3) (Wenzel, 2000). Given the relatively small sample sizes in each age class, any analysis examining prey differences by maturity or size of harbor porpoises was conducted by splitting the sizes at 140 cm, a length previously used to differentiate adults and non-adults (Wenzel, 2000).

We examined stomach contents to identify and enumerate prey and prey size through the presence of whole fish and squid (Decapodiformes) and by identification of prey by hard parts (e.g., otoliths, squid beaks, and fish jaws). These dissections generally followed the procedures outlined by Craddock et al. (2009) and Wenzel et al. (2013). We emptied the fore and main stomachs, and we separated, identified, and measured whole, relatively intact prey. We removed otoliths from intact skulls to confirm identification. Next, we examined partially digested prey to retrieve identifiable

[1] Orphanides, C. D. 2012. New England harbor porpoise bycatch rates during 2010–2012 associated with Consequence Closure Areas. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 12-19, 15 p. [Available from website.]

[2] Murphy, T., A. Kitts, C. Demarest, and J. Walden. 2015. 2013 final report on the performance of the Northeast multispecies (groundfish) fishery (May 2013–April 2014). NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 15-02, 106 p. [Available from website.]

[3] Hatch, J., and C. Orphanides. 2015. Estimates of cetacean and pinniped bycatch in the 2013 New England sink and mid-Atlantic gillnet fisheries. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 15-15, 26 p. [Available from website.]

[4] Hatch, J., and C. Orphanides. 2016. Estimates of cetacean and pinniped bycatch in the 2014 New England sink and mid-Atlantic gillnet fisheries. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 16-05, 22 p. [Available from website.]

[5] NEFSC (Northeast Fisheries Science Center). 2016. Northeast Fisheries Science Center Fisheries Sampling Branch observer operations manual 2016, 163 p. Fish. Sampl. Branch, Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA. [Available from website.]

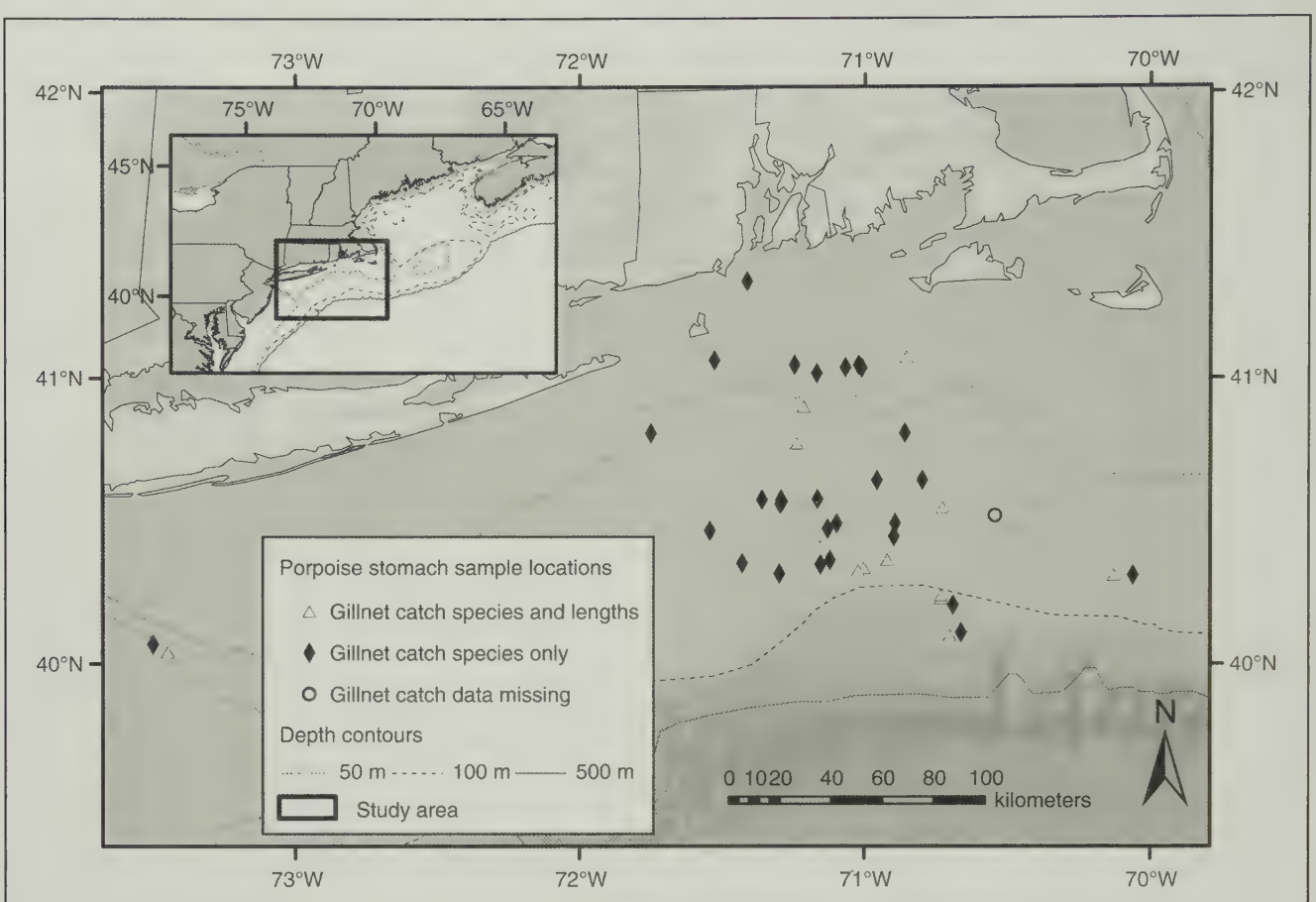

Figure 1

Map showing the 36 locations where harbor porpoises (*Phocoena phocoena*) were captured as bycatch and their stomachs (n=46) were collected by the Northeast Fisheries Observer Program, National Marine Fisheries Service, on the continental shelf off southern New England between 1994 and 2017. Sampling events are categorized on the basis of the information observers were (or were not) able to collect: species identified and length measured for gillnet catch (triangles), gillnet catch species only (diamonds), or gillnet catch data missing (circles). Depth contours are provided in meters. Sources for base map: Esri, Garmin, GEBCO, NOAA NGDC, and other contributors.

hard parts (e.g., skulls, bones, otoliths, jaws, and squid beaks). We added water to well-digested prey and separated hard parts by elutriation and by decanting them through a 0.5-mm-mesh sieve. Prey were identified to the lowest taxon possible by using Northeast Fisheries Science Center (NEFSC) reference collections, professional expertise, and published guides (Brodeur[6]; Campana, 2004).

Prey frequency and abundance

We summarized prey items by frequency of occurrence, meaning the proportion of stomachs containing a particular prey taxon (%FO), and by proportion of numerical abundance, meaning the percent occurrence of a specific prey type among all prey sampled (%N) (Wenzel et al., 2013). The occurrence and abundance of prey items were summarized by length and sex of the harbor porpoises and by 2 temporal groupings (1994–2006 and 2007–2017).

We used the vegan package (vers. 2.5-6; Oksanen et al., 2019) in R (vers. 3.6.1; R Core Team, 2019) to run a permutation analysis of variance (PERMANOVA) to test whether composition of prey species in stomachs of harbor porpoises varied by categories of sex, size, or study period. For this analysis, species counts were square-root transformed to minimize the influence of abundant species and species groups. The output of the PERMANOVA was checked for overdispersion. We also ran a similarity percentage analysis to examine the contribution of individual species and species groups to the overall Bray–Curtis dissimilarity.

Net catch

Fork lengths of fish and mantle lengths of squid found in stomach samples from harbor porpoises were compared against those from gillnet catch on hauls during which

[6] Brodeur, R. D. 1979. Guide to otoliths of some northwest Atlantic fishes. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 79-36, 70 p. [Available from Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 166 Water St., Woods Hole, MA 02543-1026.]

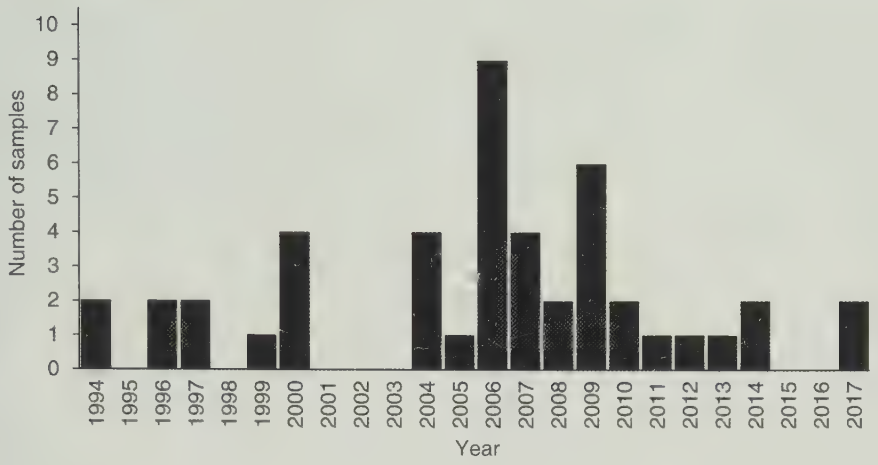

Figure 2

Distribution of the number of stomachs sampled from harbor porpoises (*Phocoena phocoena*) by year. Stomachs were collected from harbor porpoises caught incidentally as bycatch on the continental shelf off southern New England during 1994–2017.

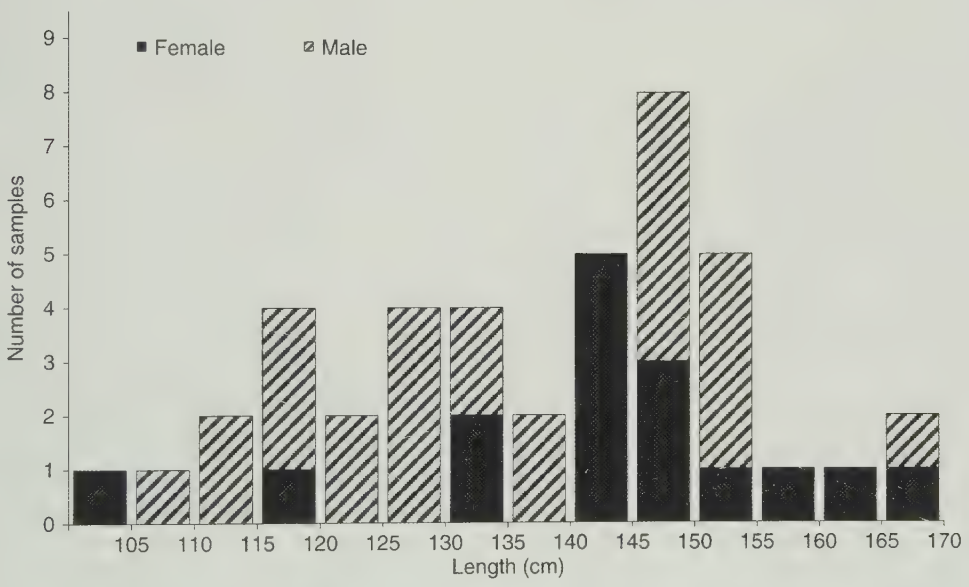

Figure 3

Distribution of the number of stomachs sampled from harbor porpoises (*Phocoena phocoena*) by total length and sex of porpoises. Stomachs were collected from harbor porpoises caught incidentally as bycatch on the continental shelf off southern New England during 1994–2017. Lengths include those for 10 harbor porpoises that were considered young of the year (<125 cm), 10 juveniles (125–139 cm), and 22 adults (≥140 cm). Lengths are not shown for one 138-cm harbor porpoise of unknown sex and for 3 porpoises of unknown maturity.

harbor porpoise stomach samples were collected. We used NEFOP data to quantify total net catch by species and length for hauls in which observers retrieved stomachs from harbor porpoises that were used in this study. Both kept and discarded net catch by species was available for 43 hauls containing 46 takes, and fish length was available for only 12 hauls completed in January, April, and May (Fig. 1). Mesh sizes of the nets for the hauls with bycatch were dominated by nets with large mesh sizes, 30.48 or 31.75 cm (12.0 or 12.5 in), with far fewer hauls of nets with

medium mesh sizes, 15.24 or 16.51 cm (6.0 or 6.5 in), and no hauls of nets with small mesh sizes (<15.24 cm), which are rare in this region. Nets with large mesh were employed on 11 of 12 hauls with recorded fish lengths. Of the 43 hauls with documented net catch, 32 hauls were conducted with large-mesh nets and 6 hauls were done with medium-mesh nets, and mesh size of nets were unrecorded for 5 hauls.

Estimation of prey lengths and weights

Fish otoliths and squid beaks found in stomachs were measured to determine lengths and weights of prey consumed. Condition of individual otoliths was rated on a scale of 0–5 following the examples of Recchia and Read (1989) and Gannon et al. (1998). A rating of 0 was applied to otoliths extracted from skulls, a rating of 1 was given to otoliths found undamaged but loose in a stomach, and ratings of 2–5 were applied to otoliths that were slightly, moderately, significantly, or severely damaged or eroded, respectively. We used otoliths with ratings of 0–2 to estimate lengths or weights of prey; these otoliths were 28% of all otoliths. All unbroken squid beaks were measured because we observed little erosion or shrinkage of the lower rostral length used to estimate squid length. If more than 25 lower squid beaks or fish otoliths of a particular taxon were present within a stomach, and of appropriate quality for measuring, we counted all samples but only measured a randomly chosen 25 samples.

We used published equations to estimate fork lengths of fish and mantle lengths of squid from otoliths and beaks for most species (Table 1, Suppl. Table [online only]) (DuPaul and McEachran, 1973; Lange and Johnson, 1981; Recchia and Read, 1989; Clay and Clay, 1991; Hunt, 1992; Froese and Pauly[7]). For species with suitable regressions, we assigned lengths from counted, but unmeasured, otoliths by resampling with replacement from measured otoliths within that same stomach sample and from that same taxon. This resampling assumed a similar size composition between measured and unmeasured otoliths and squid beaks. If no otoliths were measured for a specific species within a particular stomach, lengths were estimated by resampling with replacement from measured otoliths of that same taxon from all stomach samples.

We used fish and squid lengths to estimate biomass consumed per stomach by converting fish lengths to mass with length–weight formulas (Suppl. Table) (online only). Most fish lengths described above were converted to mass with a standard length–weight formula and coefficients from Wigley et al. (2003):

$$\ln(W) = \ln(a) + b \ln(L),$$

where W = weight (in kilograms);
a = intercept;
b = slope; and
L = length (in centimeters).

[7] Froese, R., and D. Pauly (eds.). 2019. FishBase, vers. 02/2019. [World Wide Web electronic publication; available from website, accessed February 2019.]

Table 1

List of species, identified to the nearest taxon, found in stomachs of harbor porpoises (*Phocoena phocoena*) collected by the Northeast Fisheries Observer Program, National Marine Fisheries Service, when harbor porpoises were caught incidentally as bycatch on the continental shelf off southern New England during 1994–2017.

Scientific name	Common name
Alosa aestivalis	Blueback herring
Alosa pseudoharengus	Alewife
Ceratoscopelus maderensis	Horned lanternfish
Citharichthys arctifrons	Gulf Stream flounder
Clupea harengus	Atlantic herring
Clupeidae	Clupeids
Doryteuthis (Amerigo) pealeii	Longfin inshore squid
Etropus microstomus	Smallmouth flounder
Gadidae	Gadids
Laemonema barbatulum	Shortbeard codling
Peprilus triacanthus	Butterfish
Melanogrammus aeglefinus	Haddock
Merluccius bilinearis	Silver hake
Ophidiidae	Cusk-eels
Pleuronectiformes	Flatfishes
Scomber scombrus	Atlantic mackerel
Unidentifed	Unidentified
Unidentified Decapodiformes	Squids
Urophycis spp.	True hakes
Urophycis chuss	Red hake
Urophycis regia	Spotted hake
Urophycis tenuis	White hake

If available, coefficients were applied from regional spring surveys by using both sexes of fish to best match fish found in stomach samples from harbor porpoises. No fish length–weight regression was present in Wigley et al. (2003) for Gulf Stream flounder (*Citharichthys arctifrons*); therefore, one was developed for this study with data from the NEFSC spring bottom-trawl survey conducted in 2017 (coefficient of multiple determination [R^2]=0.94, sample size [n]=29).

In the cases of the Gulf Stream flounder, the shortbeard codling (*Laemonema barbatulum*), and some taxa not identified to species, including cusk-eels (Ophidiidea), unidentified flatfish, smallmouth flounder (*Etropus microstomus*), unidentified or degraded samples of Gadidae, and other unidentified samples, no published equations for conversion from otolith length to fish length were found in the literature. No lengths were calculated for these taxa, aside from cusk-eels and Gulf Stream flounder. For both cusk-eels (R^2=0.72, n=32) and Gulf Stream flounder (R^2=0.96, n=35), otolith length–fish length regressions were calculated by using samples from the NEFSC spring bottom-trawl survey conducted in 2017. A squid beak–mantle length regression for longfin inshore squid (*Doryteuthis (Amerigo) pealeii*) was also developed by using samples from the NESFC trawl survey to ensure that

the regression represented prey samples from the same region and season as the harbor porpoise stomach samples (R^2=0.78, n=39) (Brodziak and Macy, 1996). This regression was also applied to squid of unknown species.

For some species, we could not obtain samples to develop regressions for conversion of otolith length to fish length (or weight), and none have been published to our knowledge. The otolith length–fish length regressions for Atlantic herring (*Clupea harengus*) were applied to blueback herring (*Alosa aestivalis*) and alewife (*A. pseudoharengus*) because they are in the same family. Similarly, lengths of Atlantic herring were randomly selected with replacement and were applied to 2 observations in the general clupeid category that did not have otolith length measurements. The weight regression for Atlantic herring was also applied to these 2 samples (Suppl. Table) (online only). We attempted to develop an otolith length–fish length (or weight) regression for alewife with samples from the NEFSC trawl survey but could not attain a sufficient R^2 (maximum: 0.49) with the 32 samples at our disposal. The lengths and weights of Gulf Stream flounder were applied in the same manner to the unidentified flatfish and smallmouth flounder because they are also in the same family. We applied the same otolith length–fish length (or weight) regression to all *Urophycis* species, hereafter referred to as *true hakes*, and to the unidentified Gadidae category.

An otolith length–fish length regression for horned lanternfish (*Ceratoscopelus maderensis*) yielded unreasonable size estimates (Wenzel et al., 2013). Therefore, given the small size of horned lanternfish, we estimated lengths by sampling from a normal distribution centered at a length of 5 cm with a standard deviation (SD) of 1 based on a size distribution between 3.8 and 6.0 cm, with a maximum size of 8.1 cm for mature horned lanternfish (Froese and Pauly[7]). For horned lanternfish, we estimated weights by using a Bayesian length–weight regression (Froese and Pauly[7]).

No regressions were available for shortbeard codling and for otoliths categorized as unidentified or unidentifiable. For these groups, which constituted 2% of all otoliths, we estimated lengths and weights by randomly sampling from a truncated normal distribution defined by the mean weight and SD from all prey samples. The resulting prey length distributions were compared across study periods and categories for sex and length of harbor porpoises by using Kolmogorov–Smirnov tests.

Results

Occurrence

Frequency and numerical occurrence indicate a diet concentrated on 6 species groups: squids (%FO=51%, %N=19%); red hake (*U. chuss*), white hake (*U. tenuis*), and spotted hake (*U. regia*) (%FO=43%, %N=22%); clupeids, comprising Atlantic herring, blueback herring, alewife, and clupeid samples of unknown species (%FO=34%, %N=8%); silver hake (*Merluccius bilinearis*) (%FO=32%, %N=17%); small flatfish species, including Gulf Stream flounder, smallmouth flounder, and unknown Pleuronectiformes (%FO=28%, %N=18%), and cusk-eels (%FO=30%, %N=6%) (Table 2). The combination of frequency and numerical occurrence (Costello, 1990; Amundsen et al., 1996) indicates that harbor porpoises in this region are generalist predators with true hakes and squids as the most dominant species groups (Fig. 4). However, this pooled result does not rule out potential specialization for individual harbor porpoises within the observed prey choices.

Comparison with gillnet catch

Contents of stomachs from harbor porpoises had little overlap with gillnet catch. Among 25 fish species caught in gillnets that also caught harbor porpoise used in this study, only 4 of the more rarely caught species were found in stomachs of harbor porpoises. Across 36 distinct observed hauls with porpoise bycatch, these rarely caught fish species made up 1.3% of all catch by number (both retained and discarded) and were caught in 10 hauls: haddock (*Melanogrammus aeglefinus*) in 2 hauls, silver hake in 1 haul, white hake in 1 haul, and Atlantic mackerel (*Scomber scombrus*) in 6 hauls. Only 1 species, Atlantic mackerel, was found both in the harbor porpoises caught in that net and in the net catch; Atlantic mackerel were found in 2 of 6 hauls. Dominant net-caught species (84% of catch by number), the winter skate (*Leucoraja ocellata*) and the goosefish (*Lophius americanus*), also known as monkfish, were not found in any stomachs of harbor porpoises. In addition, there was no overlap in species lengths (Fig. 5) between recorded gillnet catch and prey in stomachs of harbor porpoise (maximum prey length: 39 cm; minimum length of gillnet catch: 41 cm). The average length of 595 measured catch items was 73.6 cm (SD 11.6), far larger than any prey of harbor porpoise observed in stomach contents (mean: 11.7 cm [SD 7.7]). These 595 catch items came from 12 hauls, all but one of which were fished with 30.48-cm-mesh nets. Total weight of fish caught in pounds was recorded for most hauls, but fish lengths were recorded on relatively few hauls.

Diet composition

We examined diet composition with multiple methods. Comparison of the diet of males and females by using PERMANOVA did not indicate significant differences in species composition of prey between harbor porpoises of different sex and size (<140 cm and ≥140 cm) categories but did indicate a significant difference between study periods (1994–2006 and 2007–2017; P-value associated with the F-statistic [$Pr>F$]=0.025). Summaries of raw counts by study period and taxon contributions to the PERMANOVA indicate an apparent shift away from clupeids and toward true hakes, squids, and smaller prey (Table 3). The results of Kolmogorov–Smirnov tests indicate significant differences (P<0.001) in distributions of fish fork length and squid mantle length and in estimated biomass for the above mentioned categories of size, sex, and study period

Table 2

Summary information for fish otoliths and squid beaks found in stomachs of harbor porpoises (*Phocoena phocoena*) collected by the Northeast Fisheries Observer Program, National Marine Fisheries Service, when harbor porpoises were caught incidentally as bycatch on the continental shelf off southern New England between 1994 and 2017. Number of items, numerical abundance (%N), number of occurrences, frequency of occurrence given as the proportion of stomachs containing a particular prey taxon (%FO), and number of individuals are provided for each prey item and prey group. The count of krill prey items was recorded as not applicable (NA) because these prey items were often in pieces and therefore their presence in stomachs was noted but their number could not be accurately estimated.

Fish or squid taxon	Number of items	%N	Number of occurrences	%FO	Number of individuals
Squids	582	19.2	24	52.2	348
Longfin inshore squid	561	18.5	24	52.2	337
Unidentified squid	21	0.7	2	4.3	11
Herring species	244	8.1	16	34.8	120
Blueback herring	7	0.2	2	4.3	4
Alewife	151	5.0	6	13.0	78
Atlantic herring	84	2.8	10	21.7	37
Unidentified clupeids	2	0.1	1	2.2	1
Flatfish species	544	18.0	13	28.3	279
Gulf Stream flounder	486	16.1	8	17.4	245
Smallmouth flounder	35	1.2	1	2.2	18
Unidentified flatfish	23	0.8	5	10.9	16
True hakes	675	22.3	20	43.5	360
Red hake	220	7.3	9	19.6	117
Spotted hake	103	3.4	6	13.0	55
White hake	15	0.5	6	13.0	8
Unidentified (*Urophycis* spp.)	337	11.2	15	32.6	180
Horned lanternfish	108	3.6	1	2.2	54
Krill	NA	NA	10	21.3	NA
Unidentifiable/degraded Gadidae	17	0.6	2	4.3	9
Shortbeard codling	4	0.1	1	2.2	2
Haddock	70	2.3	1	2.2	35
Silver hake	527	17.4	15	32.6	266
Cusk-eels	172	5.7	14	30.4	94
Butterfish	4	0.1	1	2.2	2
Atlantic mackerel	30	1.0	6	13.0	17
Unidentifiable/degraded	31	1.0	14	30.4	24
Unidentified	17	0.6	6	13.0	8
Total	3025	100.0			1618

whereby fish and squid length and biomass were larger for females, large harbor porpoises (≥140 cm), and those caught during the earlier study period (weight by size: D statistic [D]=0.388; fork length by size: D=0.241; weight by sex: D=0.548; fork length by sex: D=0.438; weight by year: D=0.148; fork length by year: D=0.114). Yet these statistical differences can be challenging to interpret because of imbalances between categories, particularly because 80% of the small harbor porpoises (<140 cm) were male (Table 4).

Consumption estimates

The mean estimated prey biomass derived from otoliths and squid beaks found in a harbor porpoise stomach was estimated to be 2.35 kg (Table 5), with an SD on a per stomach basis of 2.38 kg and a median value of 1.42 kg (Fig. 6). The distribution of total estimated live prey weight per stomach is quite variable and is skewed toward 1.0 kg and less, with some high weight outliers (Fig. 6). True hakes constituted the most biomass per stomach on average (0.839 kg), and members of Clupeidae had the second-highest biomass (0.518 kg), together constituting more than half of the average estimated biomass per stomach. Squids (0.382 kg) and silver hake (0.271 kg) also contributed significantly, and together these 4 species groups (clupeids, true hakes, squids, and silver hake) constituted 85.7% of all estimated biomass. Frequently occurring but smaller prey items, such as cusk-eels and flatfish species, constituted less than 1% of estimated biomass per stomach.

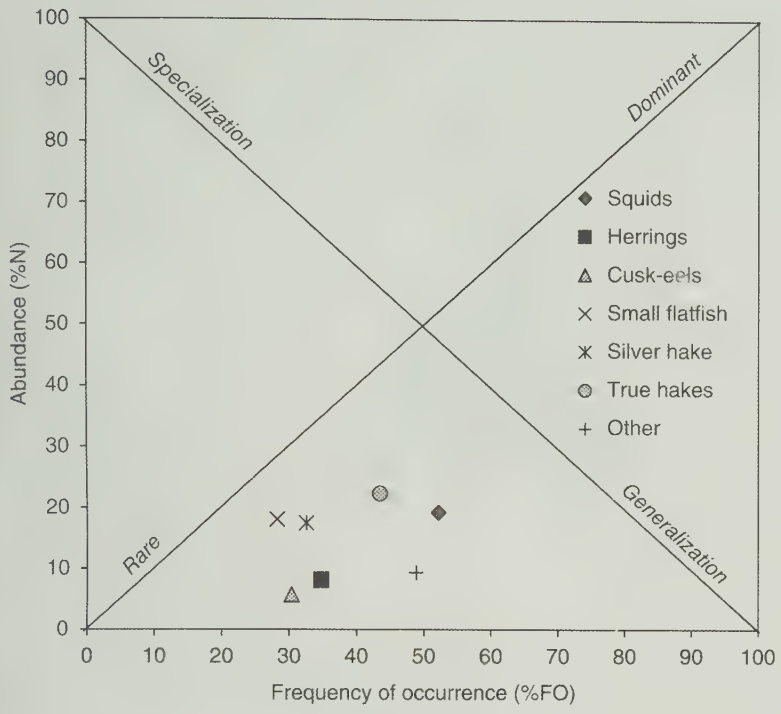

Figure 4

Costello diagram showing the relationship between abundance (%N) and frequency of occurrence (%FO) for major species groups found in stomachs of harbor porpoises (*Phocoena phocoena*) collected by the Northeast Fisheries Observer Program, National Marine Fisheries Service, when harbor porpoises were caught incidentally as bycatch on the continental shelf off southern New England between 1994 and 2017. Prey importance is expressed along the axis from the bottom left (rare) to the upper right (dominant), and feeding strategy is expressed along the axis from the bottom right (generalization) to the upper left (specialization) (Costello, 1990).

Discussion

This article provides the first analysis of the diet of harbor porpoises on the continental shelf in southern New England. It is also among the first papers in 20 years to examine the diet of harbor porpoises in the northwest Atlantic Ocean and among the first to examine diet during winter and spring months (Gannon et al., 1998). This work could take on particular relevance given a regional push toward ecosystem-based fisheries management and given potential redistribution of prey due to climate change in an area that is already rapidly changing (Nye et al., 2009; Kleisner et al., 2016, 2017; Saba et al., 2016).

Harbor porpoises as a whole were found to be generalist predators in this region during the spring and winter months, primarily feeding on clupeids, true hakes, squids, silver hake, cusk-eels, and small flatfish species. Despite the relatively small sample size available for this study, prey consumption in southern New England during the winter and spring appears to differ from that reported from previous studies conducted in the neighboring Gulf of Maine during the remainder of the year (Smith and Gaskin, 1974; Recchia and Read, 1989; Smith and Read, 1992; Gannon et al., 1998).

In southern New England, diet of harbor porpoises was more evenly apportioned—across 4 species groups, clupeids, true hakes, squids, and silver hake, which constituted 85.7% of the biomass—than the diet of harbor porpoise in the Gulf of Maine that was dominated by Atlantic herring, particularly in the summer (Table 5). One similarity between regions was the importance of silver hake, which was a common prey item in both this study and several previous studies (Smith and Gaskin, 1974; Recchia and Read, 1989; Smith and Read, 1992; Gannon et al., 1998).

Clupeids as prey items in southern New England were not as important in terms of biomass as in other regions and studies. Estimates of average biomass of true hakes per stomach of harbor porpoises from southern New England were larger than those of clupeids per stomach (840 g versus 518 g), and true hakes as a group comprised the dominant prey taxon by number and frequency (true hakes: %N=22.3%, %FO=42.6%; clupeids: %N=8.1%, %FO=34.0%). In the Gulf of Maine and Bay of Fundy, harbor porpoises were observed to depend heavily on Atlantic herring, which made up 44% of ingested biomass in the fall (Gannon et al., 1998) and 64% from June through September (Recchia and Read, 1989), compared with 22% of ingested biomass in our study. One possible reason for these differences between our work and these other studies is that the caloric value of Atlantic herring is known to increase seasonally with greater feeding and spawning in the spring and summer, contributing to their seasonal importance in the Gulf of Maine (Stevenson and Scott, 2005).

Atlantic cod (*Gadus morhua*) were also found to be primary prey items during the summer in 2 studies (Smith and Gaskin, 1974; Recchia and Read, 1989), but no Atlantic cod were present in stomach samples in our study (Table 2). The lack of Atlantic cod in stomach samples could be in part due to a decline in abundance of Atlantic cod (Pershing et al., 2015) or a result of much of the population of Atlantic cod being typically north of our study area (Fahay et al., 1999). Alternately, it may be because most of the hauls from which harbor porpoises were taken were targeting goosefish or skate (Rajidae) with nets that had a 30.48-cm mesh, whereas cod is typically caught with nets that have a mesh of 16.51 cm.

In our study, squids were frequent prey (%FO=51.1%) that constituted a significant portion of the biomass

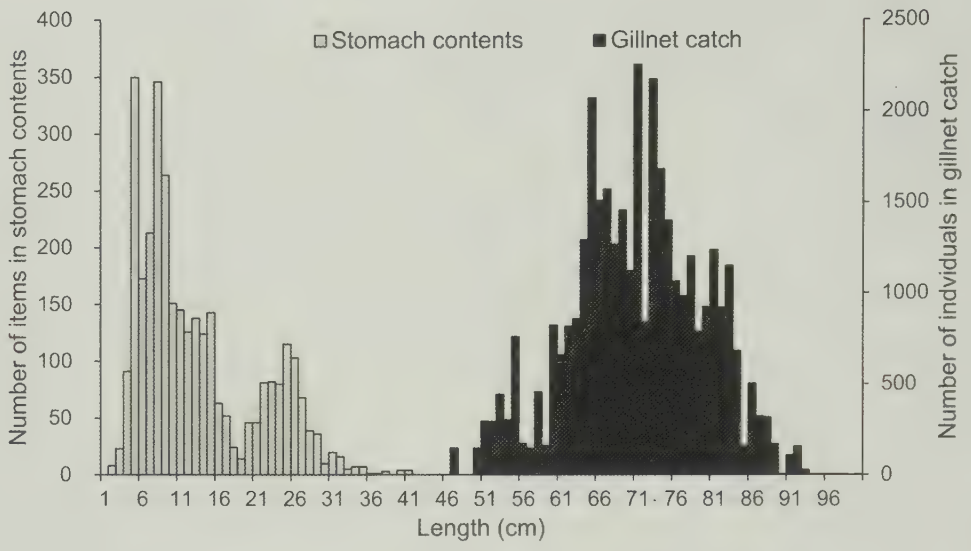

Figure 5

Length distributions of contents of stomachs (gray bars) sampled from harbor porpoises (*Phocoena phocoena*) and of catch (black bars) from gillnet hauls in which harbor porpoises were caught incidentally on the continental shelf off southern New England during 1994–2017 and for which catch length data were available. The plot is truncated so that rare length values >100 cm are not included. Lengths were estimated as fork lengths for fish and as mantle lengths for squid.

Table 3

Raw counts of species groups collected from stomachs of harbor porpoises (*Phocoena phocoena*) caught incidentally on the continental shelf off southern New England, by study period: 1994–2006 and 2007–2017. Average contributions, with standard deviations (SDs), of species groups to the permutation analysis of variance test are provided.

	Raw count		Contribution	
Species group	1994–2006	2007–2017	Average	SD
True hakes	56	619	0.17	0.17
Squids	191	391	0.14	0.15
Clupeids	207	37	0.11	0.16
Silver hake	492	35	0.09	0.14
Flatfish species	57	487	0.08	0.12
Cusk-eels	20	152	0.08	0.10
Others	29	252	0.10	0.10

Table 4

Cross tabulation of sample sizes of harbor porpoises (*Phocoena phocoena*) caught incidentally as bycatch on the continental shelf off southern New England during 1994–2017, by categories of sex, size (total length), and study period.

Study period and size	Male	Female	Unknown sex	Total
1994–2006	14	9		23
<140 cm	9	3	1	13
≥140 cm	5	5		10
Unknown size		1	1	2
2007–2017	12	8		20
<140 cm	7	1		8
≥140 cm	5	7		12
Unknown size			1	1
All years	26	17	3	46
<140 cm	16	4	1	21
≥140 cm	10	12		22
Unknown size		1	2	3

(16.2%) of prey found in stomachs of harbor porpoises caught off southern New England from January through May but were a negligible portion of the diet during the summer and fall in the Gulf of Maine (Smith and Gaskin, 1974; Recchia and Read, 1989; Smith and Read, 1992; Gannon et al., 1998). This lack of squid in the diet of harbor porpoises could be partly due to a more limited distribution of squids, particularly of longfin inshore squid, in the Gulf of Maine (Cargnelli et al., 1999a, 1999b). Small flatfish species and cusk-eels also were a significant portion of harbor porpoise diet in our work but were not seen in other studies. They were present in large numbers and

Table 5

Measurements and estimates of biomass (total weight per stomach) for prey taxa found in stomachs of harbor porpoises (*Phocoena phocoena*) collected by the Northeast Fisheries Observer Program, National Marine Fisheries Service, when harbor porpoises were caught incidentally as bycatch on the continental shelf off southern New England between 1994 and 2017. Lengths were estimated as fork lengths for fish and as mantle lengths for squid. Averages and ranges of prey length and ranges of prey weight are not provided for those taxon that did not have suitable otoliths to measure due to erosion or damage or for those for which regressions for conversion of otolith length to fish length (or weight) were not available.

	Prey length		Prey weight		Stomach contents	
Fish and squid taxon	Average (mm)	Range (mm)	Average (g)	Range (g)	Average total weight (g)	Average total weight (%)
Squids	8.0	5.6–16.5	25.7	10.7–108.4	381.5	16.2
Longfin inshore squid	7.8	5.6–16.5	24.2	10.7–108.4	347.3	14.8
Unidentified squids	12.8	5.6–16.0	71.5	46.5–102.3	34.2	1.5
Herring species	24.8	11.4–34.2	144.8	12.2–337	518.3	22.1
Blueback herring	22.7	27.6–30.1	183.5	176.4–227.6	31.9	1.4
Alewife	17.8	11.4–34.2	74.9	12.2–337.0	253.9	10.8
Atlantic herring	25.0	19.8–32.4	143.8	64.4–286.1	231.3	9.8
Unidentified clupeids			26.7		1.2	0.1
Flatfish species	5.0	1.6–12.4	0.6	0.0–5.5	7.0	<0.1
Gulf Stream flounder	5.0	1.6–12.4	0.6	0.0–5.5	6.3	0.3
Smallmouth flounder			0.4		0.3	<0.1
Unidentified flatfish			0.6		0.4	<0.1
True hakes	18.1	2.1–33.9	53.6	0.04–268.8	839.6	35.7
Red hake	22.7	10.0–27.2	74.3	5.3–117.4	378.1	16.1
Spotted hake	20.8	9.5–29.2	82.2	0.9–17.5	196.6	8.4
White hake	28.4	24.9–33.4	144.2	93.1–246.3	50.2	2.1
Unidentified (*Urophycis* spp.)	13.8	2.1–33.9	27.4	0.04–268.8	214.7	9.1
Horned lanternfish			0.8		1.9	0.1
Unidentifiable/degraded Gadidae			76.2		29.8	1.3
Shortbeard codling			44.0		3.8	0.2
Haddock	14.4	11.5–17.0	29.6	13.8–45.5	45.1	1.9
Silver hake	11.1	3.4–38.8	23.4	0.2–382.0	270.6	11.5
Cusk-eels	10.3	4.8–20.3	4.1	0.2–18.3	16.6	0.7
Butterfish	10.7	10.6–13.1	10.2	8.5–15.4	0.8	<0.1
Atlantic mackerel	25.9	19.3–39.9	200.7	56.6–628.7	148.3	6.3
Unidentifiable/degraded			65.4		68.3	2.9
Unidentified			53.9		18.7	0.8
Total	11.7	1.6–39.9	33.6	0.1–628.7	2350.3	100.0

frequency, although their caloric importance was limited because of their small sizes.

We found little direct overlap between prey of harbor porpoises and fish catch in the gillnets that incidentally caught harbor porpoises. The catch differed from prey in both size and composition. Fish targeted with gillnets may pursue the same prey as harbor porpoises (Bigelow and Schroeder, 1953). The limited mouth gape of harbor porpoises restricts their ability to prey on the large fish caught in gillnets, as does their feeding method of swallowing prey whole (Kastelein et al., 1997a).

Despite finding differences in distributions of prey biomass and length between size and sex of harbor porpoises and study period (females tend to be larger than males and have the added caloric burden of pregnancy; Read et al., 1997), we found no difference in the composition of prey species by size or sex of harbor porpoises. Our findings could be influenced by the use of length to estimate maturity, but our results do match those of previous studies that indicate no difference in prey consumed between sizes of harbor porpoises except for calves (Smith and Read, 1992; Gannon et al., 1998). Harbor porpoises in our study period (January–May) and area were post-weaning (Smith and Read, 1992; Read and Hohn, 1995).

The PERMANOVA and Kolmogorov–Smirnov tests both found differences in prey between study periods (1994–2006 and 2007–2017). Between these periods, prey of harbor porpoises in our samples shifted away from calorie-rich clupeids and toward true hakes. The

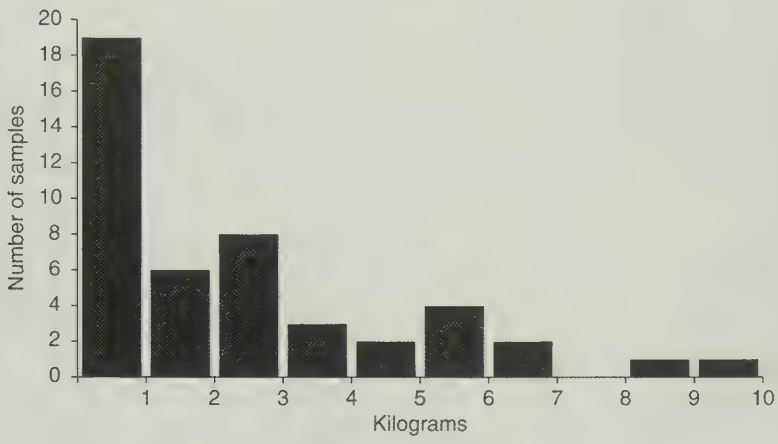

Figure 6

Histogram of estimated biomass, measured as weight in kilograms, of stomachs sampled from harbor porpoises (*Phocoena phocoena*) caught incidentally on the continental shelf off southern New England between 1994 and 2017.

diet of harbor porpoises in recent years appears to have an increased reliance on squids and a decreased focus on silver hake, and the diet is generally diversified to include more smaller species (Table 3). The differences in contributions of silver hake in the diet may be skewed by 1 sample with 314 small otoliths and another sample with 123 small otoliths. The overall differences between study periods are harder to explain but could reflect shifting species distributions due to changes in climate and regional abundance (Nye et al., 2009, 2011; Richardson et al., 2014; Doubleday et al., 2016). Shifts in diet toward smaller, less calorie-dense prey could result in future shifts in distribution of harbor porpoises or in utilization of the habitat by less-mature portions of the population.

One drawback of the reliance of a diet study on hard parts is the possibility of over-counting prey because of secondary consumption. This concern may be elevated with regard to squids, true hakes, and silver hake, which are all known to be cannibalistic (Bigelow and Schroeder, 1953; Cargnelli et al., 1999a, 1999b; Steimle et al., 1999). However, direct observation during this study of numerous partially intact small fish indicates that it would be erroneous to presume that all fish or otoliths below a particular size are secondary prey. Wisniewska et al. (2016) estimated that harbor porpoises in waters of Denmark have up to 200 prey encounters per hour during the daytime, with many of those prey measuring less than 5 cm, and as many as 550 encounters at night with a feeding success rate greater than 90%. Although the results of our study do not indicate that such consistently high rates of small fish consumption were the norm, there were 2 stomachs with over 300 small otoliths recovered, one of which contained an additional 266 squid beaks.

Using hard parts for stomach content analysis also has potential consequences for estimation of prey length and biomass. Otoliths and hard parts degraded during digestion could yield negatively biased length and biomass estimates, may favor species with larger and less fragile otoliths, and have an unknown retention time. These issues have been thoroughly discussed in the literature (see Bowen and Iverson, 2013). To minimize the influence of degraded otoliths, we followed the examples of Recchia and Read (1989) and Gannon et al. (1998) and used only minimally eroded otoliths for length and biomass estimation.

Accurate estimation of consumed biomass depends on digestion and food passage rates. The findings of Kastelein et al. (1997b) indicate passage of most solid remains from the stomach in 0.5–1.5 h, although the upper limit may depend on the type of prey eaten and the size and fragility of its otoliths and squid beaks. In seals, passage rates of otoliths and squid beaks have differed from each other and varied substantially by individual and activity level (Bigg and Fawcett, 1985; Bowen and Iverson, 2013).

We did not attempt to estimate the residence time of hard parts directly for this study, but we can back-calculate residence time by using published values of estimated daily consumption. Lockyer (2007) estimated a daily wet weight of 2.5–5.0 kg for Atlantic herring as prey and reported that the values varied by individual and time of year, and Smith et al. (2015) modeled daily consumption at 2.2 kg (80% confidence interval: 0.94–3.30). On the basis of these values, we estimated that our observed average of 2.35 kg for live weight per stomach equates to roughly 12–24 h of feeding and that the median value per stomach of 1.42 kg equates to roughly 7–15 h of feeding.

Estimates of daily consumption by species or taxa will be increasingly important as regional fisheries move toward ecosystem-based management and climate change shifts prey species distributions. For example, spring thermal habitat of red hake is predicted to move almost entirely out of southern New England within the next 20–40 years, and regional spring thermal habitat for longfin inshore squid is expected to increase by more than 200% in 60–80 years (Kleisner et al., 2017). Despite their plastic diet, harbor porpoises could be disproportionately threatened by changes in prey distribution because of their presumed high metabolism (Read and Hohn, 1995; Wisniewska et al., 2016).

The results of our study prove that harbor porpoises do not typically prey on the same species that are caught in gillnets in the study area. Without direct overlap of gillnet catch and prey of harbor porpoises, it would be difficult to use the diet of harbor porpoises to reduce bycatch. However, with improved knowledge of prey distributions, diet data could inform estimation of potential distribution of harbor porpoises and of areas of likely gear conflict.

Gannon et al. (1998) found that the diet of harbor porpoises during the fall in the Gulf of Maine was more diverse than during the summer in the Bay of Fundy, and they predicted that the diet of harbor porpoises would diversify as they move south out of the Gulf of Maine for the winter and spring. Their prediction appears to have been correct. On the basis of a relatively small sample size, we found a diet less reliant on Atlantic herring, with an increased importance of true hakes and squids. Silver hake also played a primary role in the diet of harbor porpoises, with cusk-eels and small flatfish species important on a numerical basis but not in terms of biomass. The shift toward true hakes, squids, and smaller species appears to have occurred more in the recent past, corresponding with abundance trends of Atlantic herring and squids. In the future, complementary techniques for examination of diet, such as DNA, stable isotope, and fatty acid analyses, could be paired with analysis of hard parts to better assess biases in this technique.

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Abundance of endangered shortnose sturgeon (*Acipenser brevirostrum*) in the Altamaha River in Georgia

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Abstract—Anthropogenic perturbations during the 19th and 20th centuries resulted in major declines in abundance of populations of shortnose sturgeon (*Acipenser brevirostrum*). Despite the designation of this species as endangered, most populations are still not recovering. Abundance monitoring is needed to identify fluctuations in recruitment and survival; however, river-specific assessments are deficient throughout the range of this species. During the summer of 2011, we used anchored nets to fish a closed population of shortnose sturgeon in the Altamaha River in Georgia. Mark-recapture tagging resulted in the capture of 288 shortnose sturgeon (272 fish with unique marks and 16 fish recaptured) over 11 weekly sampling occasions. Estimates of the abundance of shortnose sturgeon were derived by using Huggins closed-capture models. The preferred model incorporated effects of temporal variation on weekly capture probability and estimated an abundance of 2218 individuals (95% confidence interval [CI]: 1424–3350), including 725 (95% CI: 455–1192) juveniles and 1493 (95% CI: 954–2409) adults. Point estimates of group abundance indicate that the population is dominated by adults, although dynamic shifts in size structure following periods of high recruitment have been reported to occur. This study continued previous mark-recapture efforts in this river system, and its results offer further evidence that the Altamaha River supports the largest population of shortnose sturgeon south of Chesapeake Bay.

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The shortnose sturgeon (*Acipenser brevirostrum*) is an imperiled species that is widely distributed along the Atlantic seaboard of the United States (Vladykov and Greeley, 1963; Birstein, 1993; Kynard, 1997; NMFS, 1998). Overfishing, pollution, and habitat fragmentation during the 19th and 20th centuries led to range-wide declines in abundance and extirpations of populations of shortnose sturgeon (Dadswell, 1979). In 1967, this species was listed as endangered under the U.S. Endangered Species Preservation Act (Federal Register, 1967) and is currently protected under the U.S. Endangered Species Act of 1973. Shortnose sturgeon are listed as a single, range-wide stock, and each riverine population of this stock is separately managed; however, regulatory authorities recognize 5 regional population clusters, some of which may function as metapopulations (SSSRT, 2010). Despite decades of conservation efforts, the historical range of rivers occupied by this species is greatly reduced, and assessments that indicate recovery are rare (SSSRT, 2010; but see Bain et al., 2007).

Management of shortnose sturgeon is made difficult by a complex life history characterized by slow growth, delayed maturation, and longevity. Latitudinal differences in growth between river populations are well-documented, and the maximum age for southern populations of shortnose sturgeon (i.e., population segments south of Chesapeake Bay) has been reported as 20 years (Rogers and Weber[1]; Fleming et al., 2003), compared with the ages of northern populations that may reach 70 years (Dadswell, 1979). Likewise, although lengths at maturity of shortnose sturgeon are similar throughout their range, increased growth rates in southern river systems result in earlier ages at maturity and truncated life histories (Dadswell, 1979; Dadswell et al., 1984). Because of the difficulty of differentiating sex and maturity of fish in field conditions, a criterion of 500 mm fork length (FL) is commonly used to assign maturity for wild caught fish (Bain, 1997). Juveniles

[1] Rogers, S. G., and W. Weber. 1995. Movements of shortnose sturgeon in the Altamaha River System, Georgia, 78 p. Georgia Dep. Nat. Resour., Brunswick, GA. [Available from Georgia Dep. Nat. Resour., 2 Martin Luther King Jr. Dr. SE, Ste. 1252, Atlanta, GA 30334.]

and adults inhabit narrow reaches near the freshwater–saltwater interface of their natal rivers during the spring and summer months, dispersing upstream for spawning or foraging purposes during winter and early spring (Hall et al., 1991). Clinal differences in temperature and discharge gradients appear to be the main factors influencing river use and the timing of upstream dispersal (Hall et al., 1991; Rogers and Weber[1]; Kieffer and Kynard, 1996; Ingram and Peterson, 2018).

Current objectives for management of shortnose sturgeon are aimed at recovery of populations to minimum thresholds of population size that would allow for eventual delisting (NMFS, 1998). Because of the marked absence of historical abundance data, research must prioritize efforts to define and evaluate listing criteria for contemporary populations. The largest and best-studied populations of shortnose sturgeon occur in the Hudson River in New York (56,708 adults; Bain et al., 2007) and in the Delaware River in Delaware and New Jersey (~13,000 adults; O'Herron et al., 1993). Assessments of this species are lacking for most rivers south of the Chesapeake Bay; however, results of recent studies indicate that southern populations are particularly susceptible to declines in abundance because of their accelerated life cycle and lower abundances (Peterson and Farrae, 2011; Peterson and Bednarski, 2013; Bahr and Peterson, 2017). Therefore, the systematic monitoring of southern populations may be particularly important to identify fluctuations in annual recruitment or adult survival over multiple years.

In contrast to most large river systems along the Atlantic coast, the Altamaha River, in Georgia, is a relatively undisturbed habitat with one of the largest populations of shortnose sturgeon in the southeastern United States (NMFS, 1998; SSSRT, 2010). As such, it provides a rare opportunity to study population dynamics of shortnose sturgeon at the southern extent of the range of this species. Monitoring of the population in the Altamaha River from 2004 through 2010 identified shifts in size structure that were characterized by variable abundance of juveniles and stable abundance of adults (Peterson and Bednarski, 2013). Because southern populations may be particularly sensitive to point disturbances, continued assessments are necessary to evaluate changes in annual recruitment or adult survival. Consequently, the objectives of this study were to provide updated estimates of abundance for the population of shortnose sturgeon in the Altamaha River to complement previous work in this system.

Materials and methods

Study area

The Altamaha River is formed by the confluence of the Oconee and Ocmulgee Rivers and flows in a southeasterly direction for 207 km to its mouth at the Atlantic Ocean, which we designated as river kilometer (rkm) 0 (Fig. 1). The location of the interface of freshwater and saltwater varies depending on flow but is typically found between rkm 35 and 50 (Rogers and Weber[1]); tidal influence can persist as far as 60 rkm upstream from the mouth (Sheldon and Alber, 2002). The main channel of the Altamaha River has no impoundments below the fall line, allowing shortnose sturgeon to access a variety of habitats throughout their life history. Although juveniles and spawning adults have been documented near the confluence and in both tributaries of the Altamaha River, the Oconee and Ocmulgee Rivers, during the winter months, the estuary represents the primary habitat of shortnose sturgeon (Ingram and Peterson, 2018). During summer, individuals are primarily limited to deepwater areas of the main channel near the freshwater–saltwater interface (Rogers and Weber[1]; Peterson and Bednarski, 2013; Ingram and Peterson, 2018).

Capture and tagging

All methods for the capture and handling of shortnose sturgeon in this study were performed in accordance with relevant guidelines and regulations and were authorized by the National Marine Fisheries Service (endangered species permit no. 16482), Georgia Department of Natural Resources (scientific collecting permit no. 13791), and University of Georgia Institutional Animal Care and Use Committee (animal use protocol no. A2013 01-012-R1).

From May through August 2011, shortnose sturgeon were targeted in the Altamaha River estuary with anchored monofilament gill nets and trammel nets. Nets were deployed in the tidally influenced reach of the estuary, with the majority of sampling effort occurring below the freshwater–saltwater interface (rkm 10–35). Clean-bottom sites for netting were identified from prior studies in the system (e.g., Peterson and Bednarski, 2013; Ingram and Peterson, 2018) and were confirmed with sonar. All nets measured 91.4 m long and 3.1 m deep. Gill nets were constructed of 3 randomly ordered 30.5-m panels of monofilament meshes with stretch measures of 7.6, 10.2, and 15.3 cm. Trammel nets had an inner panel of 7.6-cm mesh surrounded by 2 outer panels of 30.5-cm mesh. Nets were fished perpendicular to the river channel for 30–60 min during slack tides to maximize capture efficiency and minimize gear damage.

Shortnose sturgeon were identified and distinguished from sympatric species according to the descriptions of Vladykov and Greeley (1963) and Scott and Crossman (1973). Captured fish were immediately transferred to a floating net pen (1.0 × 1.5 × 0.5 m) and allowed to recover until netting activities were completed. Fork length, total length, and weight were recorded, and fish were examined for internal and external tags. If no tags were found, a uniquely coded passive integrated transponder tag was inserted into the body musculature beneath the 4th dorsal scute. Once tagged, fish were released at their original capture site.

Mark-recapture analyses

Abundance estimates for juvenile and adult cohorts of shortnose sturgeon were derived by using Huggins closed-capture p and c models (Huggins, 1989, 1991). All

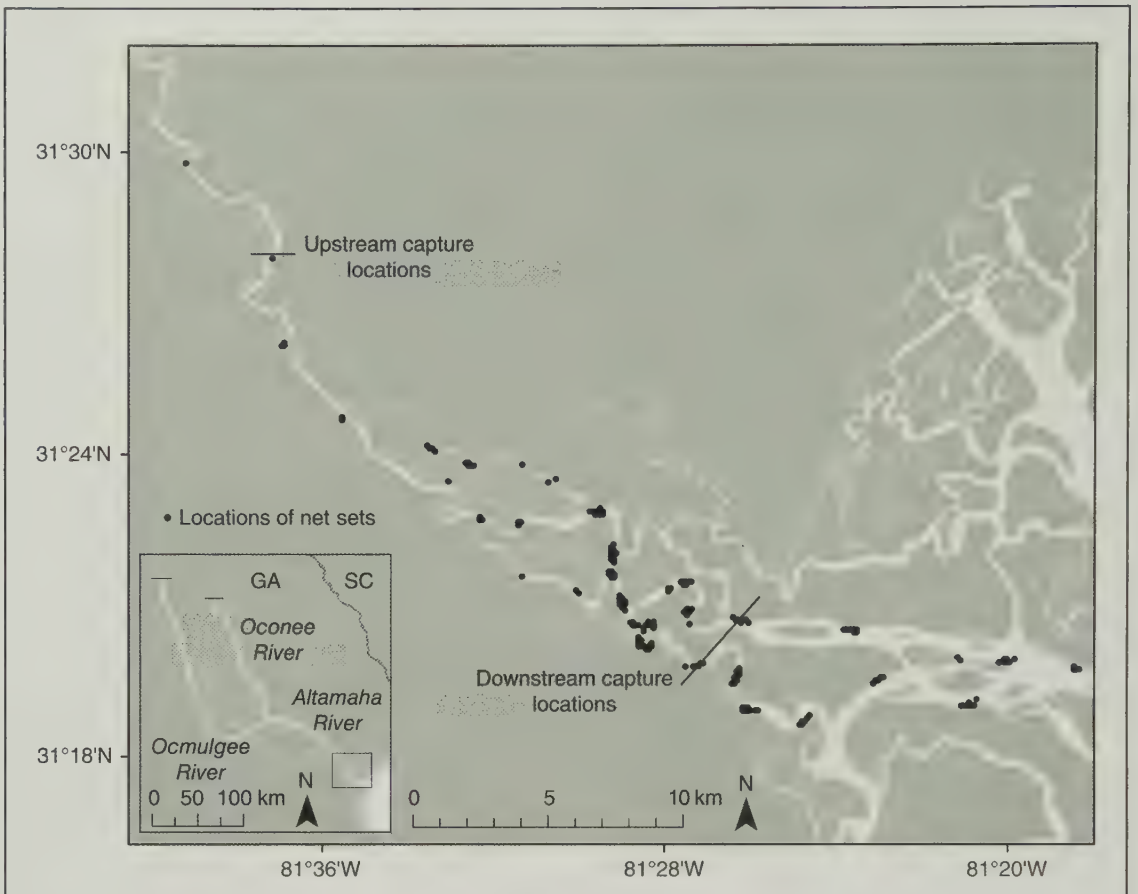

Figure 1

Map of the study area where shortnose sturgeon (*Acipenser brevirostrum*) were targeted by using unique monofilament gill and trammel nets (circles, number of nets=405) set in the Altamaha River estuary in Georgia during 23 May–5 August 2011. The lines delineate the upstream and downstream locations where fish were captured. The inset shows the relative location of the Altamaha River system in coastal Georgia. The navigable waters of the tributaries to this system, the Oconee and Ocmulgee Rivers, are shown in the inset up to the fall line in each river (horizontal lines).

models sourced the program MARK (White and Burnham, 1999) through the package RMark (vers. 2.2.7; Laake[2]) in R (vers. 3.5.1; R Core Team, 2018). Age assignments for shortnose sturgeon from length–frequency histograms are typically inextricable beyond age 1 because of increasing overlap in distribution with age (Fig. 2) (e.g., Dadswell et al., 1984; Kynard, 1997; Peterson and Farrae, 2011; Peterson and Bednarski, 2013); therefore, fish were identified as either juveniles (<500 mm FL) or adults (≥500 mm FL) on the basis of length at capture. Based on mark-recapture sampling, individual capture histories were constructed in R and were used as input data to fit models containing parameters for capture and recapture probability. Weekly sampling occasions were chosen to ensure that marked fish could randomly mix with unmarked fish before potential capture in subsequent sampling periods (Conroy and Carroll, 2009; Peterson and Bednarski, 2013).

Candidate models that assumed constant capture probability (M_0), time-varying capture probabilities (M_t), group effects (M_g), or both time-varying capture probabilities and group effects (M_{tg}) were compared by using formal model selection methods. The relative weight of evidence for each specific model was evaluated by using the Akaike's information criterion corrected for small sample sizes (AIC*c*; Hurvich and Tsai, 1989), as described by Burnham and Anderson (2002). For all models, the capture probability of marked and unmarked individuals was set as equal because of a low recapture rate (i.e., below 50%). Sampling was limited to the late-spring and summer months when the population was assumed closed (Peterson and Bednarski, 2013; Ingram and Peterson, 2018).

[2] Laake, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. Alaska Fish. Sci. Cent., AFSC Processed Rep. 2013-01, 25 p. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA. [Available from website.]

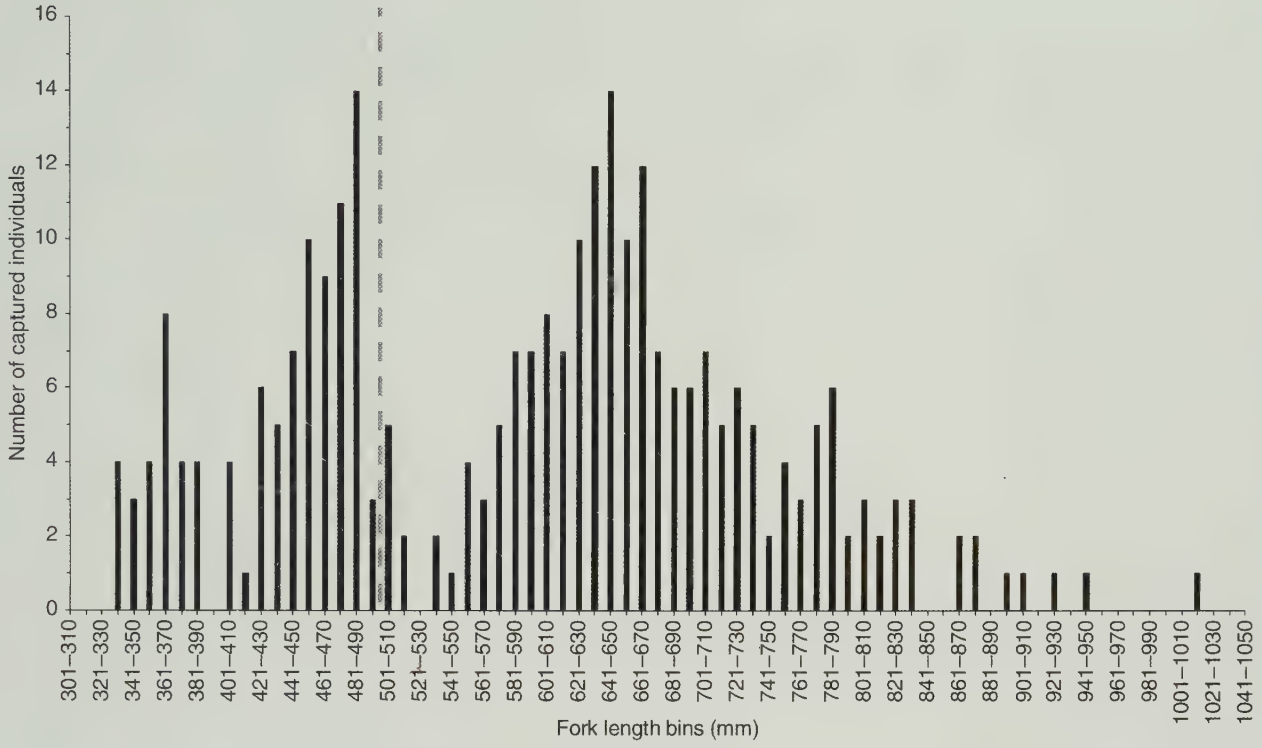

Figure 2

Length–frequency histogram of the number of shortnose sturgeon (*Acipenser brevirostrum*) that were captured in the Altamaha River in Georgia during 23 May–5 August 2011 (number of captured fish [*n*]=288). The vertical dashed line indicates the fork length used to separate juveniles (<500 mm, *n*=96) from adults (≥500 mm, *n*=192).

Results

During 2011, shortnose sturgeon were targeted with a total of 405 individual nets deployed for a total of 244.3 net hours. Sampling occurred Monday–Friday with a mean effort of 22.2 net hours/week (standard deviation [SD] 5.4), within a range of 14.2–30.9 net hours/week, over 11 weekly sampling periods from 23 May to 5 August. Net soak time ranged from 0.16 to 1.97 h, and the mean soak time was 0.61 h (SD 0.25). Netting efforts resulted in the take of 288 shortnose sturgeon, including 96 juveniles (89 fish with unique marks and 7 fish recaptured) and 192 adults (183 fish with unique marks and 9 fish recaptured) (Table 1), with capture rates of 0–19 individuals/net and a mean capture rate of 0.71 individuals/net (SD 1.70). Length of captured fish ranged from 332 to 1015 mm FL, with a mean of 595.12 mm FL (SD 140.67). Of the 272 unique fish encountered, 12 shortnose sturgeon were recaptured once during a later weekly occasion and 2 fish were recaptured twice. The total recapture rate of tagged fish over the course of the study was 5.6% (16 of 272 fish recaptured).

Results of model selection provide strong evidence for the top-ranked model based on our mark-recapture data (Table 2). The preferred model (M_t; number of parameters: 11) from evaluation with the AIC*c* is the model that incorporated effects of temporal variation on weekly capture probability of shortnose sturgeon. This model comprised ~99% of the weight in the data set and was ~100 times more likely to be the best model than the second-ranked model. There was essentially no support for the remaining candidate models that assumed constant capture probability or included group effects (i.e., relative difference in AIC*c* values between the best model and each candidate model was >10).

Estimates of abundance for shortnose sturgeon were determined on the basis of the AIC*c*-preferred model for capture probability (M_t). Modeling yielded a total point estimate of 2218 shortnose sturgeon (standard error [SE] 527.7; 95% CI: 1424–3350), with juvenile abundance of 725 individuals (SE 182.5; 95% CI: 455–1192) and adult abundance of 1493 individuals (SE 361.0; 95% CI: 954–2409). The assumption of a closed population was considered valid because regular sampling immediately upstream and downstream of the estuary reach in the study area did not result in capture of fish and indicated that violations of closure did not occur or were rare (Fig. 1). Two individual fish were determined to have died during sampling procedures; these fish with known fates were incorporated into the modeling framework during the construction of the capture histories (Table 1).

Table 1

Weekly sampling effort and number of juvenile (<500 mm fork length [FL]) and adult (≥500 mm FL) shortnose sturgeon (*Acipenser brevirostrum*) captured and recaptured in the Altamaha River in Georgia during the summer of 2011.

Sampling period	Total no. of nets set	Net hours	Juvenile		Adult	
			Captured	Recaptured	Captured	Recaptured
May 23–29	30	28.4	15	0	22	1
May 30–June 5	44	28.9	9	1	16[a]	1
June 6–12	46	30.9	8	1	33	1
June 13–19	36	19.0	3	0	12	1
June 20–26	36	19.4	7	2	18	0
June 27–July 3	38	22.0	4	1	8	2
July 4–10	43	24.9	20	2	25[a]	1
July 11–17	33	15.8	2	0	5	0
July 18–24	35	20.1	11	0	13	1
July 25–31	36	20.8	6	0	17	1
August 1–7	28	14.2	11	0	23	0
Total	405	244.3	96	7	192	9

[a] A single captured fish with a known fate that was not marked.

Table 2

Evaluation of the Huggins closed-capture candidate models used to describe variation in capture probability of juvenile and adult cohorts of shortnose sturgeon (*Acipenser brevirostrum*) in the Altamaha River, Georgia, from 23 May to 5 August 2011. Results include Akaike information criterion corrected for small sample size (AIC*c*), difference in AIC*c* between models (ΔAIC*c*), Akaike weight (w_i), and the number of parameters (K) estimated for each model. The AIC*c*-preferred model (M_t) incorporated the effects of temporal variation on weekly capture probability.

Capture probability	AIC*c*	ΔAIC*c*	w_i	K
Time (M_t)	1439.73	0.00	0.99	11
Time and group interaction (M_{tg})	1449.88	10.15	0.01	22
Constant (M_0)	1480.50	40.78	0.00	1
Group (M_g)	1481.72	41.99	0.00	2

Discussion

Population assessments remain a key research need because of their usefulness in efforts to quantify and examine the recovery of endangered shortnose sturgeon (NMFS, 1998; SSSRT, 2010). Here, we provide new information regarding demographics of shortnose sturgeon in the Altamaha River during 2011. Specifically, we estimated abundance of juveniles (725 individuals) and adults (1493 individuals) from applied mark-recapture sampling and with capture-recapture models. These abundance data add to our knowledge of this population of shortnose sturgeon and are necessary to inform development of management strategies for ensuring long-term population survival.

Conditional likelihood methods, such as the Huggins closed-capture model, are powerful tools for estimating abundance from individual encounter probabilities (Huggins, 1989, 1991). However, the validity of these parameter estimates is dependent on the underlying model assumptions, specifically that 1) the population is closed and 2) all individuals have equal capture probability (Conroy and Carroll, 2009). To minimize any inherent uncertainty in the models and to ensure that these assumptions were met, we used a sampling design consistent with previous work (i.e., Peterson and Bednarski, 2013). Although the assumption of closure is difficult to validate, the lack of captures beyond the study area, as well as limited evidence of upriver movements from acoustic telemetry detections, is consistent with the assumption that the population was closed during the sampling period (see Ingram and Peterson, 2018). Likewise, there appears to be no bias of size selection on capture probability for shortnose sturgeon in the Altamaha River (Peterson and Bednarski, 2013), and model selection results provide no evidence for group effects on capture probability between juveniles and adults.

Estimates of abundance from the time-varying capture-probability model indicate that the Altamaha River continues to support one of the largest and most persistent populations of shortnose sturgeon in the southeastern United States. However, the overall dearth of quantified assessments for other southern systems makes river-specific comparisons difficult. Analogous studies of southern populations that exceed 1000 individuals have been done only in the Savannah River in Georgia and South

Carolina (Bahr and Peterson, 2017) and in the Pee Dee River in North Carolina and South Carolina (Kynard, 1997). For the population in the Altamaha River, Peterson and Bednarski (2013) reported point estimates of annual abundance in a range of 1206–5551 individuals during summer in 2004–2010, with a between-year coefficient of variation in the river system of up to 56.6%. The noted disparity of estimates between years for the relatively undisturbed population in Altamaha River indicates that such cyclic variation is normal but may be evident only on temporal scales beyond the typical research cycle of 1–3 years. As such, we suggest that continued long-term monitoring of populations of shortnose sturgeon is necessary to develop indices of abundance and, ultimately, define management goals for recovery.

Observed demographics from our study are consistent with previously described trends and add to the multiyear data series available for shortnose sturgeon in the Altamaha River (Peterson and Bednarski, 2013). Our results indicate that the Altamaha River population continues to be largely dominated by adults, likely in response to the observed shift from a juvenile-dominated structure to one dominated by adults, following 3 years of sustained drought in 2008–2010 (Peterson and Bednarski, 2013). Variable juvenile recruitment, coupled with a relatively stable adult abundance over several years, has been attributed to rapid adult turnover following periods of high recruitment, such as the level that was observed in 2004–2007 (Peterson and Farrae, 2011; Peterson and Bednarski, 2013). The shifts in annual population structure that are readily apparent from these uninterrupted data are likely a result of the response of populations of shortnose sturgeon to stochastic environmental events (Buckley and Kynard, 1985; Jenkins et al., 1993; Rogers and Weber[1]; Woodland and Secor, 2007). As such, sustained annual monitoring may be the only way to reliably inform or evaluate management efforts for this population.

The results of this study further indicate the viability of mark-recapture methods for sampling populations of shortnose sturgeon. Although labor intensive, these methods are relatively simple to implement and provide data that can yield robust demographic estimates—particularly for populations in southern systems for which the model assumptions of closure can be met over relatively short sampling periods. Furthermore, these methods can be applied over multiyear studies to generate long-term, standardized data sets necessary for the management of long-lived species. The success of comparable multiyear mark-recapture studies of large populations of shortnose sturgeon, such as those in the Hudson River in New York (Bain et al., 2007) and in the Savannah River in Georgia (Bahr and Peterson, 2017), indicates that a standardized mark-recapture method could be strategically implemented on a coast-wide scale. However, no other populations of shortnose sturgeon have been studied on the temporal scale used to evaluate the population in the Altamaha River, for which annual estimates are available over an uninterrupted period from 2004 through 2011 from this study and another (Peterson and Bednarksi, 2013).

The utility of hydroacoustic tools to estimate abundance has been recently demonstrated for the sympatric Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) during spawning runs in rivers in New York, North Carolina, and South Carolina (Flowers and Hightower, 2015; Vine et al., 2019; Kazyak et al., 2020). Although methods that incorporate acoustic telemetry are appropriate for endangered species and benefit from being largely passive, they are currently impractical for use with shortnose sturgeon in southern river systems. Because of the logistical constraints inherent in acoustic tagging studies, sample sizes are often too small to reliably estimate abundance for a representative proportion of tagged fish (e.g., Ingram and Peterson, 2018). Likewise, the size selectivity of side-scan sonar is limited by current technological capabilities and only larger fish (>40 cm FL) can be reliably identified (Andrews et al., 2020).

The overall findings of this study have important implications for species recovery and build upon previous mark-recapture derived estimates of abundance and recruitment for shortnose sturgeon. Quantification of population demographics is a prerequisite for the accurate assessment of recovery. Although marked clinal variation among stocks of shortnose sturgeon in rivers illustrates the need to manage this species as distinct population segments, the interannual variability in demographics and recruitment of these stocks underscores the need for long-term monitoring to develop regionally specific goals for recovery. Continuation of this research within the Altamaha River is necessary to further population recovery and viability—particularly to refine threshold points for the minimum population size that can be used to evaluate the appropriateness of listing status under the Endangered Species Act and to facilitate the allocation of resources.

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General text must be typed in 12-point Times New Roman font throughout. A brief introduction should convey the broad significance of the paper; the remainder of the paper should be divided into the following sections: Materials and methods, Results, Discussion, and Acknowledgments. Headings within each section must be short, reflect a logical sequence, and follow the rules of subdivision (i.e., there can be no subdivision without at least 2 subheadings). The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be written out in full and defined the first time they are mentioned. Abbreviations should be used sparingly because they are not carried over to indexing databases and slow readability for those readers outside a discipline. They should never be used for the main subject (species, method) of a paper.

For general style, follow the U.S. Government Publishing Office *Style Manual* (2016, available at website) and *Scientific Style and Format: the CSE Manual for Authors, Editors, and Publishers* (2014, 8th ed.) published by the Council of Science Editors. For scientific nomenclature, use the current edition of the American Fisheries Society's *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* and its companion volumes

(*Crustaceans, Mollusks, Cnidaria and Ctenophora*, and *World Fishes Important to North Americans*). For species not found in the above mentioned AFS publications and for more recent changes in nomenclature, use the Integrated Taxonomic Information System (ITIS, available at website), or, secondarily, the California Academy of Sciences *Catalog of Fishes* (available at website) for species names not included in ITIS. Common (vernacular) names of species should be lowercase. Citations must be given for the identification of specimens. For example, "Fish species were identified according to Collette and Klein-MacPhee (2002); sponges were identified according to Stone et al. (2011)."

Dates should be written as follows: 11 November 2018. Measurements should be expressed in metric units, for example, "58 metric tons (t);" if other units of measurement are used, please make this fact explicit to the reader. Use numerals, not words, to express whole and decimal numbers in the general text, tables, and figure captions (except at the beginning of a sentence). For example, "We considered 3 hypotheses. We collected 7 samples in this location." Use American spelling. Refrain from using the shorthand slash (/), an ambiguous symbol, in the general text.

Cite all software, special equipment, and chemical solutions used in the study within parentheses in the general text, for example, "SAS, vers. 6.03 (SAS Institute Inc., Cary, NC)."

Word usage and grammar that may be useful are the following:

- *Aging*
  For our journal, the word *aging* is used to mean both age determination and the aging process (senescence). Authors should make clear which meaning is intended where ambiguity may arise.

- *Fish and fishes*
  The plural of the word fish (a collective noun that implies individuals without regard to species) is *fish*.
  Example: The *fish* were collected by trawl net.
  Example: The numbers of *fish* collected that season were less than the numbers from previous years.

  The plural for *fish species* is *fishes* (a contrived plural used by taxonomists to mean several or more *fish species*) or one can use *fish species* (which is preferred in this journal for clarity across disciplines).
  Example: The *fishes* of Puget Sound [biodiversity is implied] or
  Example: The *fish species* of Puget Sound [preferred plural for clarity across disciplines].

- *Crab and crabs, squid and squids, etc.*
  The plural of the word *crab* (i.e., many individuals without regard to species) is *crab*.
  Example: The crab were sorted by weight.
  Example: Many red king *crab* were dying [Many individuals of one species of crab.]

  The plural of *crab species* is *crabs* (a word used by taxonomists) or *crab species* (the latter is preferred in this journal for clarity).
  Example: These *crabs* were selected for treatment. [Different crab species are implied.]
  Example: These *crab species* were selected for treatment. [Preferred word choice for clarity of meaning.]
  Example: Snow *crabs* are found throughout the North Pacific Ocean and Bering Sea. [There are 2 species of snow crab and therefore the word *crabs* can be used here.]
  Example: *Two species* of snow *crab* are found throughout the North Pacific Ocean and Bering Sea. [Preferred usage for clarity.]
  Example: Three crabs were selected for treatment. [3 species of crab are implied.]
  Example: Three crab species were selected for treatment. [Preferred word choice for clarity.]

- *Fisherman and fisher*
  We use *fisherman* and *fishermen* in this journal not *fisher* and *fishers*. One can always use crew member, vessel operator, and angler (the latter for recreational fishing.

- *The definite article with common names of species*
  When the singular common name of a species represents the entire class or group to which it belongs, use the definite article.
  Example: Only one species of the genus *Salmo* is found in the Atlantic Ocean—*the* Atlantic salmon (*Salmo salar*).
  Example: The sonic emissions of *the* bottlenose dolphin are complex.

  For plural common names, this rule does not apply.
  Example: Chinook salmon are found throughout the Pacific Ocean.
  Example: Bottlenose dolphins are found in temperate and tropical waters.

- *Sex*
  For the meaning of male and female, use the word *sex*, not *gender*. Do not write "fish were sexed." Write, "sex was determined."

- *Participles*
  As adjectives, participles must modify a specific noun or pronoun.
  Example: Using mark-recapture methods, these scientists determined the size of the population. [Correct. The participle *using* modifies the word *scientists*.]
  Example: These scientists, based on the collected data, concluded that the mortality rate of these fish had increased. [Incorrect. The scientists were not based on the collected data.]
  Example: These scientists concluded, on the basis of collected data, that the mortality rate of these fish had increased. [Correct. The offending participle has been eliminated and an adverbial phrase modifies the verb *concluded*.]

Equations and mathematical symbols should be set from a standard mathematical program (MathType or Equation Editor). Equations formatted in LaTex are not acceptable. For mathematical symbols in the general text (α, χ^2, π, $\pm$, etc.), use the symbols provided by the MS Word program and italicize all variables, except those variables represented by Greek letters and the superscript and subscript parts of variables and expressions. Do not use photo mode when creating these symbols in the general text, and do not cut and paste equations, letters, or symbols from a different software program.

Number equations (if there are more than one) for future reference by scientists; place the number within parentheses at the end of the first line of the equation.

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Acknowledgments should be no more than 6 lines of text. Only those who have contributed in an outstanding way should be acknowledged by name. For recognition of other persons or groups, use a general term, such as *crew*, *observers*, or *research coordinators*, and do not include names with these terms.

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Tables are often overused in scientific papers; it is seldom necessary to present all the data associated with a study. Tables should not be excessive in size and must be cited in numerical order in the text. Headings should be short but ample enough to allow the table to be intelligible on its own.

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- Note probability with a capital, italic *P*.
- Provide a zero before all decimal points for values less than one (e.g., 0.07).
- Round all values to 2 decimal points.
- Use a comma in numbers of 5 digits or more (e.g., 13,000 but 3000).

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Figure legends should explain all symbols and abbreviations seen in the figure and should be double spaced on a separate page at the end of the manuscript.

Line art and halftone figures should be saved at resolutions >600 dots per inch (dpi) and >300 dpi, respectively. Color is allowed in figures to show morphological differences among species (for species identification), to show stain reactions, to show gradations (such as those of temperature and salinity within maps), and to distinguish between numerous lines and symbols in graphs. Figures approved for color should be saved in CMYK format.

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